POPULATION REGULATION OF THELASTOMATID NEMATODES (NEMATODA: THELASTOMATIDAE) OF COCKROACHES

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ABSTRACT

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Populations of thelastomatid nematodes in cockroach hosts were investigated.

The population biology, life history, habits, distribution, and gross morphology of cockroaches involved are discussed.

New species of thelastomatid nematodes from cockroaches are described and keys to species of Protrellus and Blatticola are given.

Evidence for population regulation in six species of thelastomatids in eight species of cockroaches collected from the field is presented. No host contained two adult males, infrapopulations with two juvenile males were very rare, the number of adult females per host was small, and monogamy was common. Juvenile males were rare while juvenile females were relatively common, indicating that, compared to females, males develop and are eliminated rapidly from hosts (leaving one), or that males are less common to start with. Infection prevalence varied markedly between the cockroach species.

Reproductive competition due to crowding, and cyclical egg production were found in two species. Mechanisms which may control these phenomena are discussed.

The effects of density-independent climatic factors on seasonal variation in incidence and infrapopulation structure of one thelastomatid population were transient.

Evidence for population self-regulation in Protrellus dixoni was obtained from laboratory studies. Infrapopulations were regulated by a density-dependent and sex-dependent reduction in infection intensity with infrapopulation age. This reduction was not equal in initial speed

or intensity between the sexes (reduction in number of males was faster) and led to infrapopulations with never more than a single adult male, and few adult females. In structure, these laboratory-produced infrapopulations resembled those in field collected hosts.

Unmated females produced male progeny only (probably by arrhenotokous parthenogenesis). Female offspring probably result from amphimixis.

Possible methods of thelastomatid infrapopulation regulation are discussed. It is concluded that regulation is parasite-mediated and due to chemical interference competition. Regulation benefits the surviving nematodes because per capita fecundity is greater in uncrowded infrapopulations. Self-regulation may be common among thelastomatids and other parasites.

SECTION I

INTRODUCTION

SECTION 1

INTRODUCTION

The parasitic way of life is a highly successful one followed by a great many diverse organisms. Amongst animals, parasitic groups and species have evolved apparently independently in almost every phylum. Some phyla are exclusively parasitic while others contain members that are either free living or parasitic through all or part of their life history. The nematodes, in spite of their morphological uniformity, are amongst the most abundant, successful, and ecologically diverse animals on earth (Schmidt & Roberts, 1977; Welch, 1963). They are the most successful group to have arisen from the evolutionary experiments that have occurred among the pseudocoelomic, eutelic Aschelminthes. Free living forms are abundant. Other forms have exploited the parasitic mode of existence perhaps more effectively than any other group of animals (Welch, 1963). Nematode parasites are found in all classes of vertebrates and in Echinodermata, Mollusca, Annelida, and Arthropoda (Anderson, 1984). Insect-nematode associations are particularly common and it is surprising therefore that parasitologists generally overlook the abundance and range of adaptation displayed by these (Welch, 1963). Such associations have generally been studied only at the individual host level whereas the parasite population as a whole has been virtually ignored, especially in those nematodes that are parasites of wild hosts.

Recently, it has been recognized that studies of individual host-parasite systems, while important for understanding regulation of those involved, have tended to obscure the fact that parasitism is an ecological relationship which must be expressed quantitatively in terms

of populations (Crofton, 1971). The growth of a parasite population does not differ fundamentally from the growth of a free-living animal population, and the general principles of ecology apply equally well to parasites (Nickol, 1977; Schmidt & Roberts, 1977). No population over-exploiting its resources is likely to survive. If unchecked, the growth of any population would continue exponentially until constraints began to operate. Such constraints may be density-independent and operate over the whole range of population densities, or they may be density-dependent and operate with increasing severity as the population size increases. Both types of constraint may operate upon any or all of the basic population processes of natality, mortality and recruitment. Any evidence of constraints should, where possible, be related to biotic and abiotic variables (Esch, Hazen & Aho, 1977).

To accommodate ecological parasitology, a few authors have turned their attention to creating general theories and mathematical models as frameworks within which past and future investigations may find a place. Such models have some use because they suggest what sorts of questions are important and how their answers relate to other data (Bradley, 1972). However, there is a danger that mathematical models will lead to a high level of abstraction. As Gilbert, Gutierrez, Frazer & Jones (1976) have pointed out, there are two different problems. Firstly, there is the problem of the purely theoretical worker. Many recent papers concerning parasite population biology refer only peripherally or not at all to field or laboratory data (for example, Anderson, 1974, 1982a; Anderson & Gordon, 1982; Anderson & May, 1978, 1979; Crofton, 1971; Dietz, 1982; Hirsch, 1977; May & Anderson, 1978, 1979; Nassell & Hirsch, 1972). Becker (cited by Anderson, 1982b) noted that of seventy five epidemiological models published between 1974 and 1979, only five

contained any data. Secondly, there is the problem of the laboratory worker who never ventures out into the field. It is often unknown if results obtained in the laboratory accurately or even approximately reflect the situation in the field. A further problem associated with mathematical or theoretical models erected to explain parasite populations is that generalisations are often based on data concerning parasites of vertebrates. Parasites of invertebrates are not usually considered.

One of the more acceptable recent models concerning a general theory of parasite populations is that of Bradley (1972). He diverted attention away from adaptations evolved by parasites to enhance survival, a subject which dominates older literature, to a consideration of what, given such adaptations, prevents a parasite's indefinite increase. Many host-parasite systems are relatively stable, despite the fact that both infection intensity and reproductive potential may be high. Bradley (1972, 1974) suggested that this relative stability must result from the operation of negative feedback control of the processes which affect parasite numbers and that wherever there is a redundancy of transmission above that required for mere persistence of the parasite, various stabilising mechanisms evolve. His theory (Bradley, 1972, 1974) suggested three ways in which the upper limits of parasite numbers might be determined (but not necessarily regulated):

Type 1. By transmission, where small changes in transmission rate can lead to large changes in parasite population size. It does not regulate population size because there is no negative feedback involved. Transmission determined infection is precarious and unstable, but it may be characteristic of parasites at the edge of their range or parasites of hosts with short life spans, so that parasite populations

do not build up over very long periods because of annual replacement of host stock.

Type 2. Regulation at the level of the host population through: a), a host sterile immune response, which adversely affects or eliminates the parasites in individual hosts and prevents re-infection, or b), through overdispersion (aggregation) of the parasites within the host population with subsequent death of the most heavily infected individuals. Regulation by this type is also precarious because it is very dependent on a particular host community size and structure.

Type 3. Regulation at the level of the host individual where transmission is well above the minimum for persistence of the parasite, and numbers are regulated by the individual host. This type of regulation is the most efficient because it is density-dependent and is related to two phenomena, i.e., highly efficient transmission combined with premunition, immunity, or some similar process of parasite regulation by each host. Bradley omitted a consideration of regulation by inter- and intraspecific competition between parasites, a mechanism which should be included in this category. Type 3 regulation is seen, to a varying degree, in very many parasitic systems where parasite numbers are maintained about some level by a variety of tactics (Holmes, Hobbs & Leong, 1977; May, 1973).

As Hirsch (1977) has pointed out, models are probably best tested by researchers other than those who have constructed them. The aim of this thesis is to investigate which, if any, of Bradley's proposed three types of regulation occur amongst thelastomatid nematodes of cockroaches. While remaining within the framework of Bradley's model, it attempts to redress the recent imbalance in the field of parasite population ecology by presenting empirical data from both field and laboratory studies of a

group of invertebrate parasites. It presents evidence that cockroach thelastomatids regulate their own populations by a density- and sex-dependent reduction of infection intensity, leading, unusually, to underdispersed distribution patterns.

Most sections of this thesis are presented in the form of papers (two of which have been published and two of which are in press). This format has resulted in some unavoidable repetition. The papers are linked by preambles.

SECTION II

THE HOSTS

SECTION II

THE HOSTS

A) INTRODUCTION

i) General introduction

Apart from taxonomic descriptions and collection records, little has been published concerning the biology and life-history of native New Zealand cockroaches. In order to understand better the relationships of thelastomatids in cockroaches, the population biology, general biology, and seasonal occurrence of some of the native hosts was studied (Section II, B, C). Insufficient collections of other native cockroaches preclude host population analysis, but information concerning their habitats, distributions, and general biology is included (Section II, D).

Exotic cockroaches investigated for thelastomatids were Blattella germanica L. and Drymaplaneta variegata (Shelford, 1909). Blattella germanica has been extensively studied by other workers. The habits and life history of this cockroach are discussed in Section II, E. Nothing has been published concerning the biology or life-history of Drymaplaneta variegata, a cockroach introduced to New Zealand (probably from Australia) and now established in the North Island. This species was used as a host for experimental research into thelastomatid populations (Section IV, F). Information concerning the habits and life history of the cockroach, obtained during this research, is presented in Section II, E.

ii) Taxonomy

Cockroaches are a widely distributed order of exopterygote neopteran insects in the order Blattodea (Mackerras, 1970) which were formerly associated with mantids, grasshoppers, crickets, and stick insects in the old order Orthoptera. It has been estimated that there are about 3,500 species of cockroach in 450 genera (Cornwell, 1968) but Roth & Willis (1960) consider that at least 4,000 remain to be described.

A taxonomic summary of the New Zealand cockroaches is given below, following the system of Johns, 1966. The number of species in each genus is noted, but the specific names of only those cockroaches investigated in this study are given. All except four are endemic to New Zealand. Introduced species are indicated by an (I) after their name.

Suborder Blaberoidea

Family Chorisoneuridae

Celeriblattina (2 species)

Suborder Blattoidea

Family Blattidae

Celatoblatta (13 species)

C. vulgaris Johns, 1966

C. peninsularis Johns, 1966

C. quinquemaculata Johns, 1966

C. brunni (Afken, 1901) Johns, 1966

Platyzosteria (2 species)

Periplaneta (1 species) (I)

Drymaplaneta (1 species)

D. variegata (Shelford, 1909) (I)

Suborder Epilamproidea

Family Blattellidae

Ornatiblatta (1 species)

Parellipsidion (3 species)

P. pachycercum Johns, 1966

Blattella (1 species)

B. germanica L. (I)

Shawella (1 species) (I)

iii) General biology of cockroaches studied

All species of cockroach studied here are nocturnal and remain hidden during the day beneath bark, stones, holes or galleries in living or dead timber, or other refugia. They are oviparous and protect their developing eggs in a hardened ootheca which they carry for variable periods, then deposit or glue to surfaces in their environment (Fig. II, A, 1). When incubation is complete, the ootheca splits along the dorsal edge and the nymphs are released. The nymphs resemble the adults in external morphology (but without wings), and live in the same habitat with them in loose aggregations. They undergo a varying number of moults to reach maturity. The number of moults undergone by cockroaches in each species is probably fixed within certain limits. Like other cockroaches, native species are probably detritivorous and coprophagous.

iv) The alimentary canal

The alimentary canal of all species studied is of the same general pattern. The foregut is a narrow oesophagus, followed by an enlarged crop in which food is stored. Posterior to the crop is a thick walled proventriculus with plates or teeth which serve to break up food.

Figure 11, A, 1

Oothecae of Parellipsidion pachycercum (arrow 1) and Celatoblatta peninsularis (arrow 2) glued to bark of Fuchsia excorticata.

(Scale line in mm.)

The midgut is a narrow tube lined with a delicate peritrophic membrane, and has diverticula or caeca at the anterior end. Between the midgut and the hindgut is a pyloric region from which arise the Malpighian tubules. The hind gut consists of an anterior, narrow ileum bearing short spines, an enlarged, inverted-flask-shaped colon, a short, narrow isthmus, and a posterior, enlarged rectum which has six rectal pads. In cockroaches, water is resorbed in the rectum when in short supply, and there is a movement of ions between the hind gut and the haemolymph (Bell & Adiyodi, 1982; Cornwell, 1968; Guthrie & Tindall, 1968). Similar hindgut activities probably occur in cockroaches considered here. Most faecal material is deposited in the form of discrete faecal pellets. Only occasionally was faecal material too fluid to form a pellet.

Both the foregut and hindgut have a thin cuticular lining which is shed at each moult. In some cockroaches (Lee, 1960), the hindgut dries before moulting, leading to an increase in osmotic pressure. In newly moulted cockroaches in this study, the hindgut did not appear to dry out, and was often full of faecal material immediately after the moult. The peritrophic membrane of the midgut, which moves posteriad enclosing the food in insects (Chapman, 1969), does not form an envelope around the food in the colon of these cockroaches and so must be broken up anterior to this.

v) Parasites other than thelastomatids

Apart from the thelastomatid nematodes discussed later (Section III, Section IV), all native species hosted mites on intersegmental membranes (probably the cosmopolitan Tyrophagus putricentii, M. E. McIntyre, Department of Zoology, Victoria University, Wellington, New Zealand, pers. comm.); gregarines (probably a Gregarina species; Eugregarinida: Cephalina) in the midgut; unidentified gordian worms

(Nematomorpha) in the haemocoel; bacteroids in the fat bodies and ovaries; and bacteria in all regions of the gut. However, none of the cockroach species examined had flagellate or ciliate protozoans in the gut. In other cockroaches, such protozoan symbionts are common associates. Drymaplaneta variegata has a parasite fauna similar to that of native species, but no gordian worms were found. Apart from thelastomatids, the parasite fauna of Blattella germanica was not noted.

B) SEASONALITY IN A FIELD POPULATION OF TWO NEW ZEALAND COCKROACHES (BLATTODEA).

Figures 1-11 in this paper are referred to in the list of figures and elsewhere in the text as Figures II, B, 1-11.

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Abstract A population comprising *Celatoblatta peninsularis* and *Parellipsidion pachycercum* was sampled from Banks Peninsula, New Zealand over 1 year. Sub-adult cockroaches were assigned to 6 size classes (probably instars) by interocular distance and hind femur length. *P. pachycercum* was most abundant in December and January and adults were abundant in most months. In contrast, *C. peninsularis* was most abundant from February to June and adults were rare except in November. Adult females were less abundant than adult males in both species. Although both species may be bivoltine, they use difference overwintering strategies.

Keywords cockroaches; binomials; Blattidae; Blattellidae; life cycles; population structure; size distribution; seasonal variations

INTRODUCTION

Apart from taxonomic descriptions (e.g., Johns 1966) and collection records, very little has been published on the endemic cockroaches of New Zealand. There are many publications on the life histories of laboratory-reared cockroaches outside New Zealand (e.g., Willis et al. 1958) but few observations appear to have been made on the life histories of roaches in the field. Life history data were obtained from a series of samples of cockroaches taken (primarily for parasitological research) at about monthly intervals from Kaituna Valley, Banks Peninsula.

Only 2 endemic roaches are known from Banks Peninsula. *Celatoblatta peninsularis* Johns, 1966 (Blattidae) is confined to Banks Peninsula and occurs in several habitats, including tussock, scrub, open forest, and stony areas (Johns 1966). *Parellipsidion pachycercum* Johns, 1966 (Blattellidae) is widely distributed in the wetter and cooler parts of the South Island, in a variety of habitats (Johns 1966). The 2 species are sympatric on Banks Peninsula in the foliaceous bark of the native tree fuchsia (*Fuchsia excorticata* (J. R. et G. Forst.) Linn. f.) which is common in Kaituna Valley.

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METHODS

Nymphs and adults of *C. peninsularis* and *P. pachycercum* were collected from the bark on trunks of fuchsia trees growing within 10 m of the stream at the end of the Kaituna Valley Road, Banks Peninsula, Canterbury, New Zealand (43°43′15″S, 172°45′30″E; elevation 250 m). Collections were made once every 5 weeks from 1 March 1981 to 21 February 1982 and an approximately equal volume (about 0.4 m^3) of bark was removed from about 10 trees on every collection date, different trees being sampled on each occasion. As fuchsia bark has paper-thin layers, great care was taken in sorting through this material in the laboratory to ensure that all roaches were removed.

Roaches were killed by crushing the nerve cord behind the head, and then viewed with a stereomicroscope. Interocular distance (the minimum distance between the eyes) and hind femur length of sub-adults were measured to the nearest 25 μm, using an eye-piece graticule. The (brachypterous) adults were not measured.

Although the sex of roaches can sometimes be determined as early as instar 1 (Snodgrass 1937, Amerson & Hays 1967) and I was able to do so at least for instar 2 (Fig. 3, 4), sub-adults were not sexed routinely in this work, although the sex ratio was noted in class 6 and for adults. Rapid dissection was necessary for the parasitological aims of the project and therefore developing reproductive structures were destroyed, especially in smaller nymphs.

RESULTS

All animals, including the smallest nymphs, could be identified to species by differences in head and abdominal markings. The vertex, frons, and clypeus of *P. pachycercum* (Fig. 1) have dark, vertical,

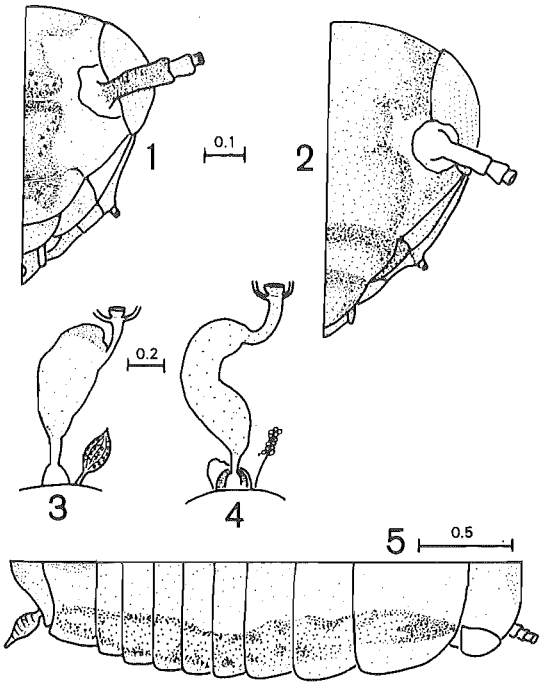

Fig. 1–5 *Parellipsidion pachycercum* and *Celatoblatta peninsularis*: (1) head, class 1 nymph, *P. pachycercum*; (2) head, class 1 nymph, *C. peninsularis*; (3) hind gut, *P. pachycercum* class 2 ♀; (4) hind gut, *C. peninsularis* class 2 ♂; (5) *P. pachycercum*, class 1 nymph, entire. Measurements in mm.

median bands whereas *C. peninsularis* (Fig. 2) has no such patterning. The dorsal and ventral abdomen of *P. pachycercum* are distinctly mottled (Fig. 5), but the abdomen is almost uniformly dark brown in *C. peninsularis*. There are also internal differences. The hind gut of *P. pachycercum* nymphs is shaped like an inverted flask, and is fawn with a greenish 'cap' (Fig. 3); that of *C. peninsularis* is almost uniform in diameter and it is fawny yellow (Fig. 4).

Size classes

For sub-adults, plotting interocular distance against hind femur length gave 6 clusters for both *Parellipsidion pachycercum* (Fig. 6) and *Celatoblatta peninsularis* (Fig. 7). Size classes 1 to 4 were distinct and probably represent instars, but classes 5 and 6 were indistinct. For the life history analysis, half of the individuals in the overlapping region were assigned to class 5 and half to class 6.

Adults were the most abundant class throughout the year in *P. pachycercum*, but they were the least common class in *C. peninsularis* (Fig. 8). In both species, more adult males were collected than were adult females (sex ratio for *P. pachycercum*, 1:1.71; for *C. peninsularis* 1:2.5). Overall, classes 2, 3, and 6 of both species were abundant, but there were few in classes 1, 4 (*C. peninsularis*), and 5 (*P. pachycercum*).

Seasonal abundance

There was some seasonal variation in the percentage of each species in each sample (Fig. 9). Small numbers of both species were collected from early winter to late spring (July–November). *P. pachycercum* was abundant in early summer (December 1981–January 1982), whereas *C. peninsularis* was abundant in early autumn and winter (March, June 1981) and in late summer (February 1982).

Life history patterns

Parellipsidion pachycercum Despite all size classes having occurred in all months, a growth pattern can be inferred from the data (Fig. 10). There were 2 main cohorts. One consisted of nymphs which appeared in late summer and overwintered in class 2, 3, or 4, each class becoming progressively more abundant from autumn to early spring. Later classes developed more rapidly with the onset of warmer weather and gave rise to adults in late spring. A second cohort which developed rapidly through all classes during summer may have arisen from eggs laid by these adults.

Celatoblatta peninsularis Adults were abundant in late spring, but were infrequent or absent in other months (Fig. 11). Two main cohorts were also noted. One arose from the class 1 nymphs which appeared in early summer and these developed rapidly during the warmer weather. Nymphs overwintered in class 6 and adults became abundant in November. The second cohort arose from class 1 nymphs which appeared in late summer. These developed slowly and many overwintered in classes 2 and 3 (class 2 nymphs decreased in number, and class 3 nymphs increased, through winter). Class 6 nymphs appeared by summer as a result of the rapid development of nymphs in warmer weather, but these either failed to mature, or moved elsewhere.

Oothecae Oothecae are tanned capsules produced by female cockroaches to protect a cluster of eggs. In some species (e.g., *Blattella germanica* and *Blaberus craniifer*), oothecae are carried by the female until the young are about to emerge (Guthrie & Tindall 1968, p. 99). *P. pachycercum* and *C. peninsularis* produced and deposited oothecae amongst fuchsia bark throughout the year. Those of *C. peninsularis* were larger (6.2×3.9 mm) than those of *P. pachycercum* (4.9×2.7 mm), although they were similar in shape and in colour (dark brown). *C. peninsularis* oothecae contained 10–12 developing

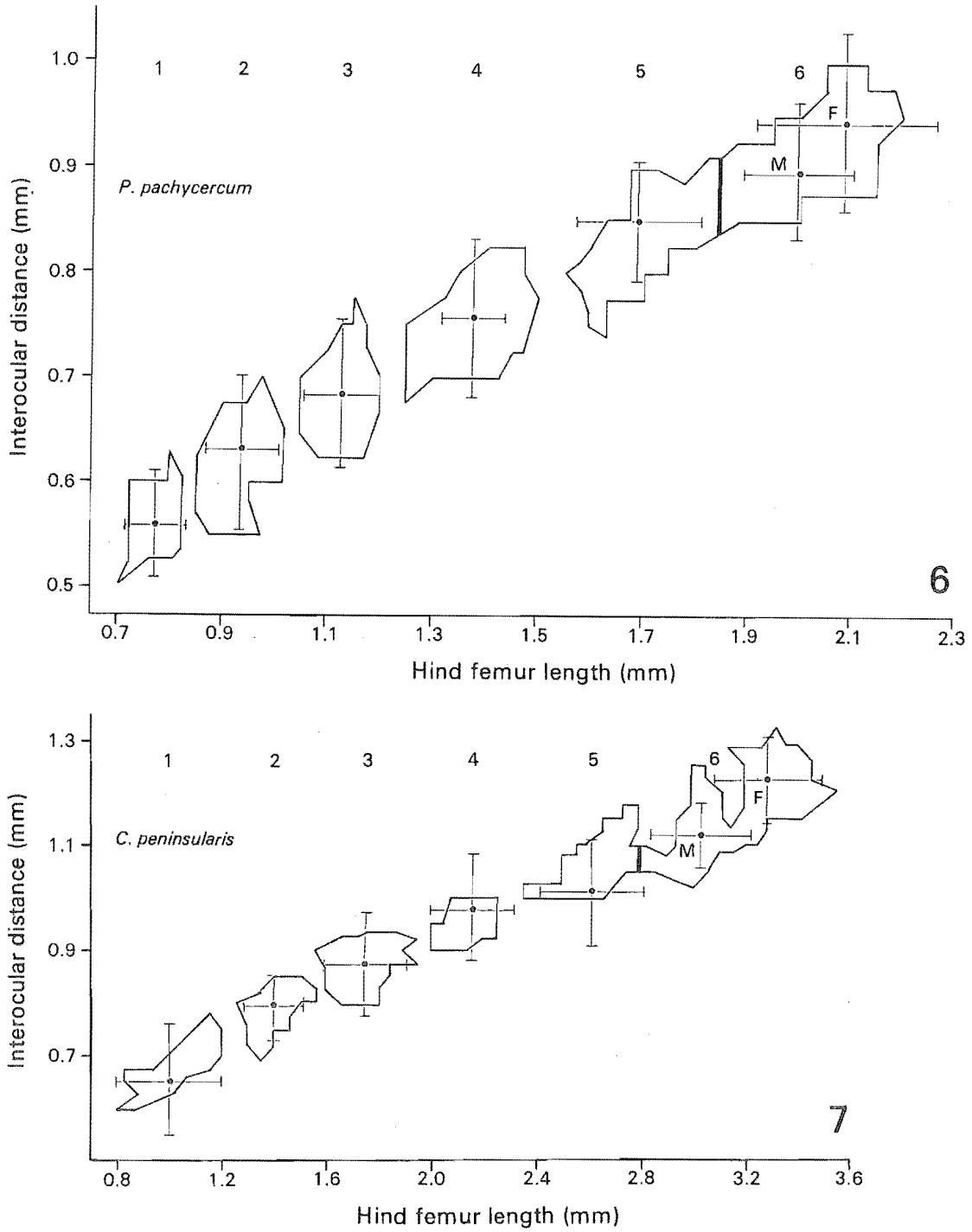

Fig. 6, 7 (6) *Parellipsidion pachycercum*; (7) *Celatoblatta peninsularis*. Sub-adult size class groups (1–6), showing extreme boundaries (continuous outer enclosing lines), means, and 95% confidence intervals of each group (*n* in each size class as in Fig. 8). M, size class 6 ♂; F, size class 6 ♀. Wide vertical band between classes 5 and 6 is an arbitrary division between the groups.

nymphs, whereas the smaller oothecae of *P. pachycercum* contained 12–14. Some oothecae had been deposited loosely and fell out when the layers of bark were separated; others were 'glued' to the bark. Some were also camouflaged with small pieces of bark glued on to their outer surfaces.

DISCUSSION

Parellipsidion pachycercum was nearly 3 times as abundant as *Celatoblatta peninsularis* in fuchsia bark at Kaituna Valley. Whether this reflects the relative abundance in the entire population is not known as the canopy was not investigated. However, few roaches were found in other habitats searched and it is therefore likely that the bark is a major habitat of both species. The probable 7 instars (at least 6 sub-adult, plus terminal instar) proposed for *C. peninsularis* and *P. pachycercum* agrees with the findings of Willis et al. (1958) and Brown (1980) for *Blatella germanica*, *B. vaga*, *Ectobius lapponicus*, and *E. pallidus*, but many European species have more.

There may be 2 reasons for the blurring of size classes 5 and 6. Firstly, the adult females of both species are larger than the adult males and this sexual differentiation may result in less defined, and possibly overlapping, clusters. Secondly, some roaches and other insects can have a variable number of instars, which may enable them to reach a species 'norm' for adult size (Tanaka 1981). Seamans & Woodruff (1939) found that the number of moults undergone by *Blattella germanica* was influenced by diet and injury. Gier (1947) found that *Periplaneta americana* had a variable number of instars and that dietary deficiency delayed or stopped moulting; Willis et al. (1958) found that *Pycnoscelus surinamensis* could have 8–12 instars. Therefore the overlap between clusters 5 and 6 possibly reflects a difference in the number of moults undergone by some individuals.

The unbalanced sex ratio found in adults of both species was not reflected in the sex ratio of the penultimate class, which was close to 1:1, as has been found in adults of other species of roach (Willis et al. 1958). Adult females may move away from the fuchsia bark habitat and therefore not have been sampled.

Numbers in each successive size class can be expected to decline because of moult failure, predation, and other factors. Willis et al. (1958) found that maturation success varied with the species but from their data I estimate that an average of 79.7% of roaches (in 12 species) reached adulthood under laboratory conditions. Poor survival of nymphs could have been the reason for the few adult *C. peninsularis* found or, alternatively, adults may favour the canopy and therefore were not collected. Conversely, sub-adult *P. pachycercum* may favour the canopy and adults the trunks, making the latter the most frequently collected group. The life span of adult *P. pachycercum* could also be longer than that of any of its nymphal stages and this is strongly supported by 3 adult *P. pachycercum* having survived for 550 days in the laboratory.

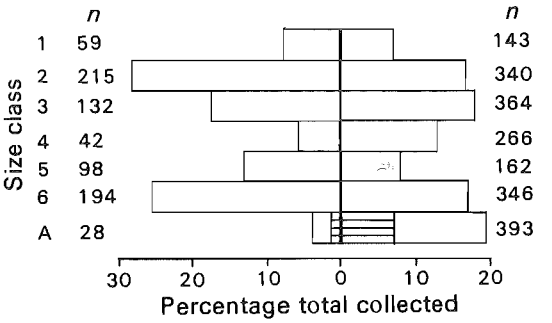

Fig. 8 Percentage of the total number of roaches collected over year in each size class (*n*, numbers per class). Left of heavy line, *C. peninsularis* (n=768); right, *P. pachycercum* (*n*=2014). (1–6, nymphs; A, adults — horizontal shading, ♀; open, ♂).

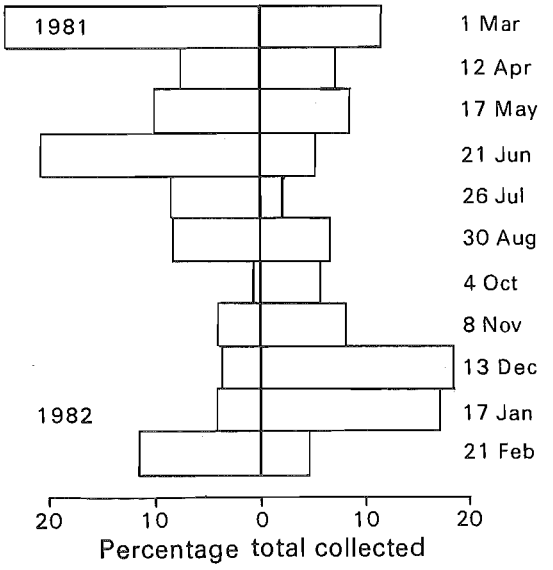

Fig. 9 Percentage of the total number of cockroaches collected in the year on each collection date (*n* for each date same as Fig. 10, 11). Left of solid line, *C. peninsularis*; right, *P. pachycercum*.

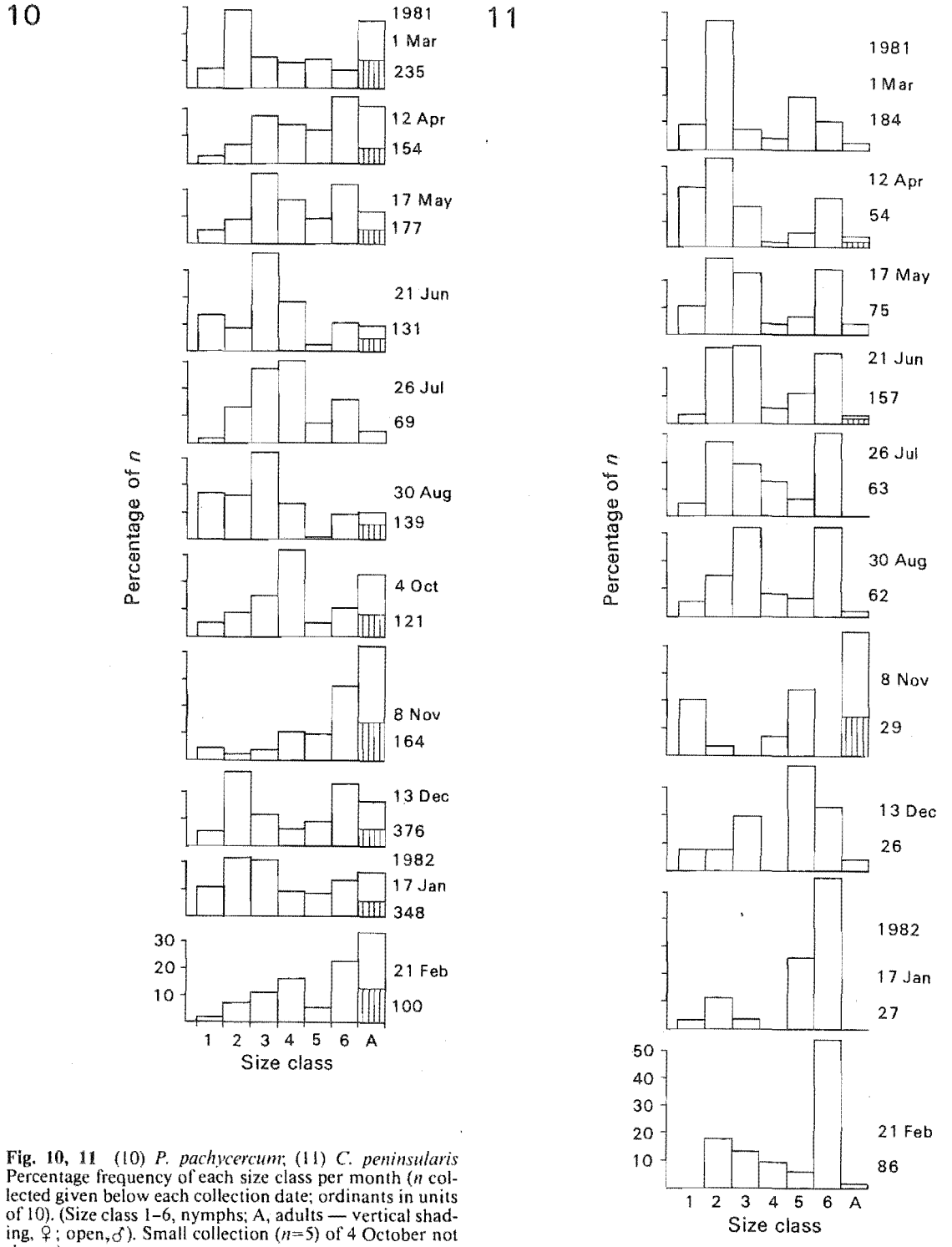

Fig. 10, 11 (10) *P. pachycercum*; (11) *C. peninsularis* Percentage frequency of each size class per month (*n* collected given below each collection date; ordinants in units of 10). (Size class 1–6, nymphs; A, adults — vertical shading, ♀; open, ♂). Small collection ($n=5$) of 4 October not shown).

Considering the larger numbers of sub-adult *C. peninsularis* found in December, January, and February, it was surprising that so few adults were seen. It is possible that they, and all classes of *P. pachycercum* suffered high mortality in those months because of unseasonably low rainfall in Canterbury — it was 56% below average between November 1981 and February 1982 (Christchurch Meteorological Office). This would be in accordance with the findings of Brown (1980) and Cornwell (1976, p. 461) that egg success and roach numbers are reduced by low humidity and drought.

Size class analyses indicated that both species may be bivoltine with 2 major cohorts per year. However, these were not clearly defined and most size classes of both roach species were present in all months. Continuous development is typical of at least some other orthopteroid insects in New Zealand (Cary 1981, Richards 1961, 1973) and a winter diapause is unusual in New Zealand endemic insects (Watt 1973). Oothecae of *P. pachycercum* and *C. peninsularis* probably, and nymphs certainly, do not diapause. Development, however, may have been slowed in certain classes (2, 3, and 6) during the colder months of the year. This is unlike the situation described for several non-domesticated species of roach in Europe, none of which is known to be bivoltine. They may be univoltine instead, overwintering only as oothecae, or semivoltine with an overwintering ootheca and a variety of quiescing or diapausing nymphal instars (Brown 1980).

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C) NOTES ON THE SIZE DISTRIBUTION OF A NEW ZEALAND COCKROACH, *Celatoblatta vulgaris*

Abstract: Populations of *Celatoblatta vulgaris* were sampled over a three year period from a variety of collection sites. Sub-adult cockroaches were assigned to 5 size classes (probably instars) on the basis of interocular distance and hind femur length. Membership of size classes increased with increasing size class so that adults were markedly more abundant than any class of nymph, and large nymphs were more abundant than small nymphs. Adult males were more abundant than adult females.

INTRODUCTION

Few observations have been published on the life histories of endemic New Zealand cockroaches. Zervos (Section II, B) found that sub-adult *Celatoblatta peninsularis* Johns, 1966 (Blattidae) and *Parellipsidion pachycercum* Johns, 1966 (Blattelidae) fall into six size classes (probably instars) when grouped according to interocular distance and hind femur length. Recently, life history data were obtained for another blattid cockroach, *C. vulgaris* Johns, 1966, collected from a number of sites.

MATERIAL AND METHODS

Adult *Celatoblatta vulgaris* Johns, 1966, (n= 285) were collected in various seasons during 1981-1984 from beneath the bark of beech trees (*Nothofagus* sp.) and from fallen timber in *Nothofagus* forests at Maruia Springs and Reefton (Buller), Craigieburn, Castle Hill, Cass, Klondyke Corner and Mt. White (Hurunui), and from galleries in dead branches of manuka trees (*Leptospermum soparium* J.R. et G. Forst.) at

Charming Creek (Nelson). Nymphs (n=160) collected with adults were assumed to belong to C. vulgaris as no other cockroach species was collected at these sites. Nets were placed against trunks below bark to be searched, or under timber and branches before these were searched, to ensure that all cockroaches, including the smallest, were collected.

Cockroaches were killed by crushing the nerve cord behind the head, then viewed with a stereomicroscope. Interocular distance (the minimum distance between the eyes) and hind femur length of sub-adults were measured to the nearest 25μm, using an eye-piece graticule. The (brachypterous) adults were not measured. Only ultimate nymphs were sexed in this study.

RESULTS

For sub-adults, plotting interocular distance against hind femur length gave 5 clusters (Fig. II, C, 1). Size classes 1 to 3 were distinct and probably represent instars, but classes 4 and 5 were indistinct because of a narrow zone of overlap. For the purposes of population analysis, half of the individuals in the overlapping region were assigned to class 4 and half to class 5. Size class 1 was the least abundant class while adults were the most abundant class (Fig. II, C, 1). This was true at all collection sites, regardless of seasons. In size class 5 (the ultimate nymphal class), the female to male sex ratio was approximately 1 : 1, but amongst adults, males predominated (female to male ratio, 1 : 1.6). Seasonal analysis of populations can not be made because collections at any one site did not occur in all seasons.

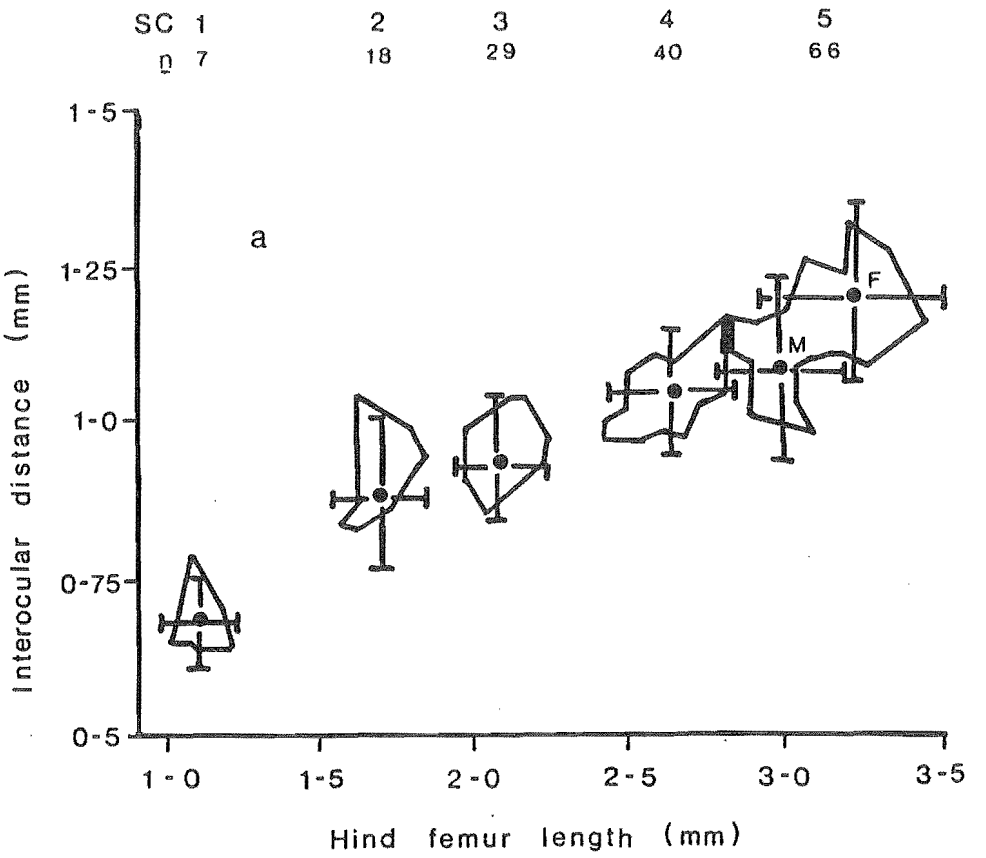
Oothecae: Oothecae (tanned capsules produced by females to protect a cluster of developing eggs) were found beneath bark at all

Figure II, C, 1

Celatoblatta vulgaris.

a), sub-adult size class groups (SC 1-5), showing extreme boundaries (continuous outer enclosing lines), means, and 95% confidence intervals of each group (n in each size class, below SC number). M, size class 5 males; F, size class 5 females. Wide vertical band between classes 4 and 5 is an arbitrary division between groups.

b), percentage of all cockroaches collected between 1981-1984 in each size class (n as for a.). Class 1-5, nymphs; A, adults (n= 285). Vertical shading in 5 and A, female; blank, males.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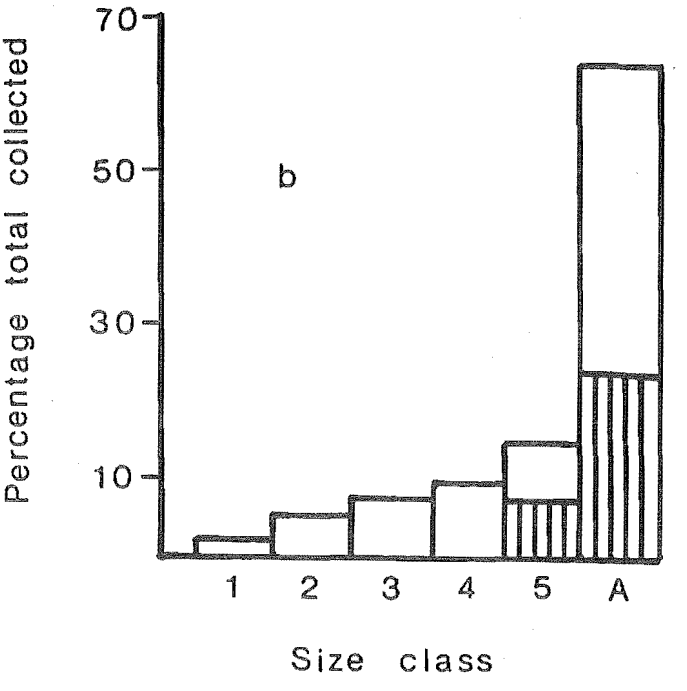
70
50
30
10
Percentage total collected
b
1 2 3 4 5 A
Size class

sites, regardless of season. Most were "glued" to bark or tree trunks, but some were loose and fell out when bark was lifted. Capsules measured 6.75 x 3.8mm and contained 12-14 developing nymphs.

DISCUSSION

Celatoblatta vulgaris is the most widely distributed of all endemic cockroaches and is usually abundant wherever it is found (Johns, 1966). The probable 6 instars (at least 5 sub-adult, plus adult) is one less than the 7 instars proposed for Celatoblatta peninsularis and Parellipsidion pachycercum (Section II, B). This is surprising because C. vulgaris and C. peninsularis are very closely related species (P. M. Johns, Department of Zoology, University of Canterbury, New Zealand, pers. comm.). Possibly, C. vulgaris size classes 4 and 5 are an amalgam of 3 instars. C. vulgaris oothecae, although similar in size to C. peninsularis oothecae (Section II, B), contain more eggs. C. vulgaris resembles C. peninsularis and P. pachycercum in that adult males outnumber adult females, and the ultimate and penultimate juvenile size classes overlap. Possible reasons for similar phenomena in C. peninsularis and P. pachycercum were discussed in Section II, B and may apply equally to C. vulgaris.

Numbers of cockroaches in each successive size class should be expected to decline (Section II, B) not increase as in C. vulgaris. Abundance of C. vulgaris adults is in direct contrast to that in C. peninsularis, where adults form the least abundant class, but is similar to P. pachycercum, in which adults form the largest class (Section II, B). Adult C. peninsularis are very seasonal in appearance (most are found in late spring, Section II, B) but C. vulgaris adults are abundant in all seasons. The predominance of adults in collections could reflect a longer adult life span compared to nymphal life span

and/or the majority of nymphs may reside in habitats not searched and may thus have avoided capture.

C. vulgaris was active wherever and whenever found, and oothecae are apparently deposited throughout the year. Continuous activity and continuous deposition of oothecae also occur in C. peninsularis and P. pachycercum, and in some other orthopteroid insects in New Zealand (Section II, B).

D) OTHER NATIVE COCKROACHES

i) Celatoblatta quinquemaculata Johns, 1966

C. quinquemaculata is known only from the alpine zone of some Otago ranges (Johns, 1966). Specimens were collected from well-aerated and drained spaces beneath boulders above the tussock line on the Rock and Pillar Ranges near Middlemarch, central Otago. Vegetation in this area is sparse, with large areas of exposed rock and smaller stones. Cockroaches were found in loose aggregations with the weta, Hemideina maori (Pictet et Saussure, 1891)(Orthoptera: Ensifera: Stenopelmatidae). The bare appearance of the surfaces beneath the rock and the large accumulation of cockroach and weta faecal pellets suggested that the same sites were used regularly as refugia (B. O'Brien, pers. comm.).

ii) Celatoblatta brunni (Afken, 1901) Johns, 1966

C. brunni is one of the smallest species in the genus Celatoblatta. It is known only from areas of scrub and stones on the Chatham Island Group (Chatham Island, Pitt Island, Southeast Island, The Sisters) (Johns, 1966). Specimens studied were collected from fallen timber at Tuku Valley, Chatham Island, and were abundant in such material (J. West, pers. comm.).

iii) Celatoblatta undulivitta (Walker, 1868)

C. undulivitta is distributed throughout most of the North Island south of Waipou, and is found in the South Island as a beach litter inhabitant of West Nelson (Johns, 1966). C. undulivitta prefers very moist conditions and is often found in sodden logs.

E) EXOTIC COCKROACHES

i) Blattella germanica Linn.

This cockroach is the most cosmopolitan domiciliary species known and is abundant wherever found (Cornwell, 1968; Guthrie & Tindall, 1968). It aggregates in mixed age groups in concealed areas or refugia in warm, moist environments, forming closely knit groups or clusters. Group formation is influenced by temperature, shelter height, and the production of aggregation pheromone (Bret, Ross & Holtzman, 1983).

Females produce oothecae containing from 29-40 eggs (number of eggs per ootheca decreases with cockroach age). Oothecae are carried by females until the young are about to emerge, or, in some cases, the young emerge while the ootheca is still attached to the female (Cornwell, 1968). Thus B. germanica differs from all other cockroaches in this study, which deposit their oothecae long before nymphal emergence. There are 5-7 moults (depending on diet, crowding, and injury) and 36-60 days between egg and adult (Amerson & Hays, 1967; Seamans & Woodruff, 1939; Willis et al., 1958). The variable number of moults observed is thought to enable B. germanica to attain a certain standard size when they become adults (Tanaka, 1981).

ii) Drymaplaneta variegata (Shelford, 1909)

The taxonomic history of this species in New Zealand is confused. It has been variously named Platyzosteria (Melanozosteria) soror, Platyzosteria soror, and Drymaplaneta semivitta (Anon, 1973; Hayes, 1975; Perrott, 1970; Ramsay, 1975), but these names are incorrect for the species established in New Zealand (P. M. Johns, pers. comm.).

Cockroaches collected at Gisborne, North Island, New Zealand, and used to establish laboratory cultures for this study (Section IV, F), were identified as D. variegata by P. M. Johns. The species is easily distinguished from other large species of cockroach in New Zealand by the white border on the three dorsal thoracic segments.

D. variegata is found from Midway Island to Tonga and New Caledonia, and from Singapore to Easter Island (Perrott, 1970); in south-western Western Australia (Mackerras, 1968); and is now widespread throughout the North Island of New Zealand from Auckland to Wellington (Hayes, 1975; M. E. McIntyre, pers. comm.). It is numerous in stacked material, woodpiles, rubbish heaps, poultry sheds, dog kennels, and similar outbuildings, and in flax grasses, palms, vines and other plants (Anon, 1973). It is often found in houses, where it attaches its oothecae to curtaining and other suitable materials (M. Dixon, pers. comm.) and is generally a nuisance (J. West, pers. comm.).

D. variegata is easily bred in captivity on a varied and unspecialized diet with adequate water (see Section IV, F). It has a variable number of instars (10-14) and takes from 5 months (usually when uncrowded in large rearing cages) to 12 months (usually when over-crowded in small containers) to attain maturity at room temperature. Over-crowding is known to adversely effect the growth rate and survival of other cockroaches (Chauvin, 1946; Griffiths & Tauber, 1942; von Landowski, 1938: Pettit, 1940). Oothecae are produced once every 3 or 4 days and unmated females produce oothecae for several weeks after their ultimate moult if deprived of a male. It is unknown if, as in some other cockroaches (Guthrie & Tindall, 1968), unfertilised eggs are viable. Oothecae measure about 8.80 x 3.90mm and are dark brown, sharply pointed at one end and rounded at the other, and contain 13-16 eggs.

Othecae are deposited loosely or are attached to surfaces, and are often partially or completely disguised with chewed and regurgitated material covering their exposed surface. Nymphs emerge after 40-50 days at 20°C. During moulting, the cockroach is usually attached head down on a vertical surface. The cuticular lining of the foregut and hindgut are cast with the rest of the exoskeleton. Cast exuviae are eaten almost immediately by the newly moulted cockroach. Newly moulted cockroaches are white but darken within a day. D. variegata, like other cockroaches (eg., Periplaneta americana (Linn.) - Glaser, 1927; Wharton, Miller & Wharton, 1954; B. germanica - Ebeling & Reierson, 1974; Sugawara, Kurihara & Muto, 1975) has an acute sense of smell and can detect very small amounts of food or water over a distance of at least 500mm.

SECTION III

THE PARASITES

SECTION III

THE PARASITES

A) INTRODUCTION

All of the nematodes in populations studied during the course of this work belong in the Thelastomatidae (Oxyurata: Oxyuroidea). A brief account of the history and taxonomy of thelastomatids is given (Section III, B). Except for Blatticola blattae (Graeffe, 1860) Chitwood, 1932, the nematodes studied were undescribed. In order to ease discussion, the nematodes are described here. They include Blatticola monandros Zervos, 1983 (Section III, C); Protrellus dixoni (Section III, D); Protrellus dalei, Blatticola barryi and Suifunema mackenziei (Section III, E). B. blattae is discussed in Section III, F. Some observations made of developing P. dixoni within eggs are presented in Section III, G. The use of the term parasite and not commensal to describe thelastomatids is discussed in Section III, H.

B) BRIEF HISTORY AND TAXONOMY OF THELASTOMATIDS

The first thelastomatid reported from a cockroach was Oxyuris diesingi (= Hammerschmidtiella diesingi (Hammerschmidt, 1838) Chitwood, 1932), described by Hammerschmidt (1838) from the intestine of Blatta orientalis L. One hundred years later in a revision paper, Chitwood (1932) described or redescribed 25 thelastomatid species from cockroaches. Since Chitwood's synopsis, the known species of cockroach thelastomatids has risen to about 200.

Taxonomic interpretations of nematodes are many and varied. As the higher classification of the nematodes is not the concern of this thesis, that given in Schmidt & Roberts (1977) is accepted without discussion.

Phylum Nematoda

Class Phasmidea

Order Oxyurata

Superfamily Oxyuroidea: The Oxyuroidea form an extensive group of morphologically diverse but probably monophyletic parasites which are best considered as saprophytes adapted to internal parasitism (Anderson, 1984; Inglis, 1965; Maggenti, 1978). The group is largely restricted to terrestrial hosts, although there are some abberant and atypical species in freshwater fish. They are well represented in insects.

Oxyuroids have phasmids but only poorly developed amphids with small, simple pores near or on the lips. They have three lips, but these are often reduced or absent. The oesophagus has a posterior valve, and the excretory system has one or two lateral canals. The egg often has an operculum. The male usually has one or two small spicules, but these are sometimes absent. The life cycle is direct and there are no intermediate hosts involved.

Family Thelastomatidae Travassos, 1920: The thelastomatids differ from other members of the Oxyuroidea in the possession of eight single submedian head papillae or labiopapillae. Other oxyuroids have four single or double papillae (Poinar, 1975). The male has a single spicule, or none, and one to four tail papillae.

C) Blatticola monandros N. SP. (NEMATODA: THELASTOMATIDAE) FROM THE BLATTELLID COCKROACH Parellipsidion pachycercum.

Figures 1-14 in this paper are referred to in the list of figures and elsewhere in the text as Figures III, C, 1-14. The reference to Rao & Rao, 1965 is referred to as Rao & Rao 1965a elsewhere in the text and in the full reference list at the end of the thesis.

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Abstract *Blatticola monandros* n.sp. occurs in the hind gut of nymphs and adults of the endemic New Zealand cockroach *Parellipsidion pachycercum*. It is distinguished from all other species of *Blatticola* in morphology — both sexes are smaller, the oesophagus is proportionately longer, and the spicule is shorter. The size of the nematode increases with the size of the host.

Keywords nematodes; Thelastomatidae; *Blatticola monandros*; new taxa; gut parasites; *Parellipsidion pachycercum; Blattellidae*

INTRODUCTION

Platyzosteria novaeseelandia Brunner, 1865 is the only New Zealand native cockroach reported to contain thelastomatid nematodes (Dale 1966). It may contain either *Blatticola tuapakae* Dale, 1966 or *Protrellus* (= *Protrellina*) *gurri* (Dale, 1966), but not both. Recently *Parellipsidion pachycercum* Johns, 1966, a brachypterous endemic cockroach (Epilamproidea: Blattellidae) of wetter and cooler parts of the South Island of New Zealand (Johns 1966) was found to harbour a new species of *Blatticola*. *P. pachycercum* occurs sympatrically in places with another indigenous roach, *Celatoblatta peninsularis* Johns, 1966 (Blattoidea: Blattidae). *C. peninsularis* is parasitised by an undescribed thelastomatid in the genus *Protrellus*. As *P. pachycercum* never contains this *Protrellus* species, and as *C. peninsularis* never contains the *Blatticola* species, it is assumed that these undescribed nematodes are host-specific. The *Blatticola* species is described here. Apart from *B. tuapakae*, 3 other species of *Blatticola* have been described: *B. blattae* (Graeffe, 1860) Chitwood, 1932, a species with a confused taxonomic history (Chitwood 1930, Dale 1966) from *Blatella aegyptiaca* L., *B. germanica* L., *Ectobia lapponica* L., and *E. livida* Fabr. (Basir 1956); *B. supellaimae* Rao & Rao, 1965 from *Supellaima* spp.; and *B. opisthoplatia* Ahmed & Jabin, 1966 from *Opisthoplatia orientalis* (Burmeister).

MATERIAL AND METHODS

Over a 12-month period, 2014 *Parellipsidion pachycercum* were collected from the exfoliating bark of the native tree *Fuchsia excorticata* (J.R. et G.Forst.) Linn.f., which is common at Kaituna Valley, Banks Peninsula. Immature roaches (n =1621) were assigned to 6 subadult size classes according to their interocular distance and hind femur length. Of the adult roaches, 145 were females and 248 were males. Roaches killed by crushing the nerve cord behind the head were dissected in cockroach saline. Some living nematodes were observed in saline in wax-sealed preparations (Doncaster 1962). All nematodes were eventually heat-killed, fixed in TAF, processed using Seinhorst's (1959) glycerol/ethanol method, and mounted in anhydrous glycerine. Measurements were taken from fixed specimens, and are given here in µm. The adult male and female nematodes described are from adult male and female hosts only.

DESCRIPTION

Superfamily OXYUROIDEA

Family THELASTOMATIDAE

Genus *Blatticola* Schwenk, 1926

Blatticola monandros n.sp. (Fig. 1-14)

Measurements of the type specimens are given in Table 1. Males (Fig. 1 and 2) 500-920 long, females (Fig. 11-14) 1400-2740; body cylindrical, of fairly uniform diameter but tapering anteriorly and posteriorly. Tail conical with a shallow constriction in female (Fig. 13), in male tapering with 2 pronounced constrictions (Fig. 2). Cuticle annulated; annuli more evident anteriorly than posteriorly, and

more evident in female than male. Head (en face) in female with a circular stoma (Fig. 11) surrounded by 4 large and 4 small papillae. Myolabia not evident. Amphidial apertures small, circular. Head in lateral view (Fig. 12) with lips offset. Buccal capsule small, width 20 in females. Oesophagus indistinctly sclerotised (especially in males) at anterior end, with distinct corpus, isthmus, and bulb (Fig. 1 and 14). Corpus subparallel-sided, expanded posteriorly; bulb valvate, with sculptured plates. Nerve ring just anterior to corpus/isthmus junction; mean length from anterior end 190 in females, 119 in males. Intestine somewhat expanded anteriorly around oesophago-intestinal junction, especially in females, decreasing in width posteriorly. Excretory pore posterior to oesophago-intestinal junction, in females just behind anterior flexure of ovary, in males about one-quarter of maximum body width from oesophago-intestinal junction, anterior to anterior flexure of testis (but not visible in all specimens). Rectal glands distinct, at junction of posterior intestine and rectum (female) or at cloaca (male).

Female (Fig. 11–14). First cuticular annulus 10–15 wide, subsequent annules about 5 apart. Tail very short, conical except for a shallow constriction; apex acute. Cuticle of tail tip thickened to form a distinct and characteristic pattern of the internal body wall in optical section (Fig. 13). Vulva in posterior sixth of body, approximately 300 from posterior end, leading to ovijector. Uterus single, directed forward from ovijector, reflexed near anterior flexure of ovary then running posteriorly to join ovary between vulva and anus. Ovary directed anteriorly, passing beneath intestine anterior to excretory pore and then reflexed dorsally to end about halfway down body (Fig. 14). Eggs asymmetrically ovoid, broader at opercular end; L 124 ± 10, W (max.) 51 ± 10; operculum distinct; surface ornamented; usually laid at 2- to 4-cell stage, but very rarely with developed larvae. Development to larval form occurs within 48h in eggs laid in saline (Fig. 3–6).

Male (Fig. 1 and 2). Cuticle distinctly annulated only anteriorly, at intervals of about 2. Head papillae not obvious. Oesophagus and intestine as in female, except intestine sometimes constricted near proximal end of testis, behind flexure. Testis single, reflexed to end about halfway down body. Nature of ejaculatory duct not evident. Spicule small, single, almost straight, broadest at middle, tapering to a point proximally and distally; capitulum and gubernaculum absent. Lateral papillae distinct, 1 pair pre-anal, 2 pairs post-anal. Tail acutely tapering, with 2 pronounced constrictions; apex an acute, cuticular mucro-like process (Fig. 2).

Larva (Fig. 7–10). Immature females could be assigned to 3 size classes; L_4 females have a developing gonad, uterus, and vulva. Immature males have a fully developed spicule, but no testis. They could not be assigned to size classes as there was too much overlap in measurements.

Type data. **Holotype** ♀, **allotype** ♂, and 24 **paratypes** (12 ♀, 12 ♂) in New Zealand National Nematode Collection, Entomology Division, Department of Scientific and Industrial Research, Auckland (holotype ♀, NZNNC holotype no. 114; allotype ♂, NZNNC 1961; 12 paratype ♂♂, NZNNC 1962-73; 12 paratype ♀♀, NZNNC 1974-85). Remainder of paratypes in Zoology Department, University of Canterbury, Christchurch. **Type host:** *Parellipsidion pachycercum* Johns, 1966; anterior end of colon of hind gut. **Type locality:** Kaituna Valley, Banks Peninsula, South Island, New Zealand (43°43′15″S, 172°45′30″E); elevation 250 m.

Remarks. The specific name *monandros* (Greek, 'one male') alludes to the presence of not more than a single adult male in established infections. The male may be accompanied by from 1 to 4 adult females; the average number of nematodes per infected roach is 1.92. Analysis of the structure of the nematode population is in progress.

Both sexes are slightly shorter than the smallest *Blatticola* so far described, *B. blattae* (male 500–920 μm, female 1440–2740 μm, against 780–1000 μm and 2000–3000 μm respectively in *B. blattae*), and are markedly shorter than the other 3 species. The spicule is also the shortest in the genus. *B. monandros* can be further distinguished by the presence of distinct rectal glands in both sexes, by the length of the oesophagus (proportionately longer in all species except the female of *B. opisthoplatia*), and by the characteristic thickening of the female's tail. Eggs are usually either 2-celled when laid, as in *B. opisthoplatia* (Ahmed & Jabin 1966) or 4-celled as in *B. tuapakae* (Dale 1966) and *B. blattae* (Bozeman 1942, Cali & Mai 1965). They are rarely 1-celled as in *B. supellaimae* (inferred from the figure in Rao & Rao (1965)). Female type specimens may contain eggs with fully developed larvae because larval development continues even after fixation. Only one live female laid eggs containing larvae. This female may have been near death and hence retained eggs to a late stage of development. In *B. tuapakae*, *B. supellaimae*, and *B. opisthoplatai* the male corpus is expanded anteriorly, unlike that of *B. monandros* or *B. blattae*. As in *B. tuapakae* and *B. supellaimae* but unlike *B. blattae* and *B. opisthoplatia* the testis is reflexed. *B. monandros* and *B. tuapakae* have 3 pairs of tail papillae, whereas the remaining species have 4 pairs.

Figure 1-14 (= Figures II, C, 1-14)

Blatticla monandros from Parellipsidion pachycercum.

(1) male, entire; (2) tail, male; (3-6) eggs, showing stages of juvenile development; (7) juvenile of unidentified sex; (8-10) L_{2-4} females; (11) female, en face view; (12) head, female, lateral view; (13) tail, female, showing vulva and anus; (14) female, entire.

(Scale lines in μm.)

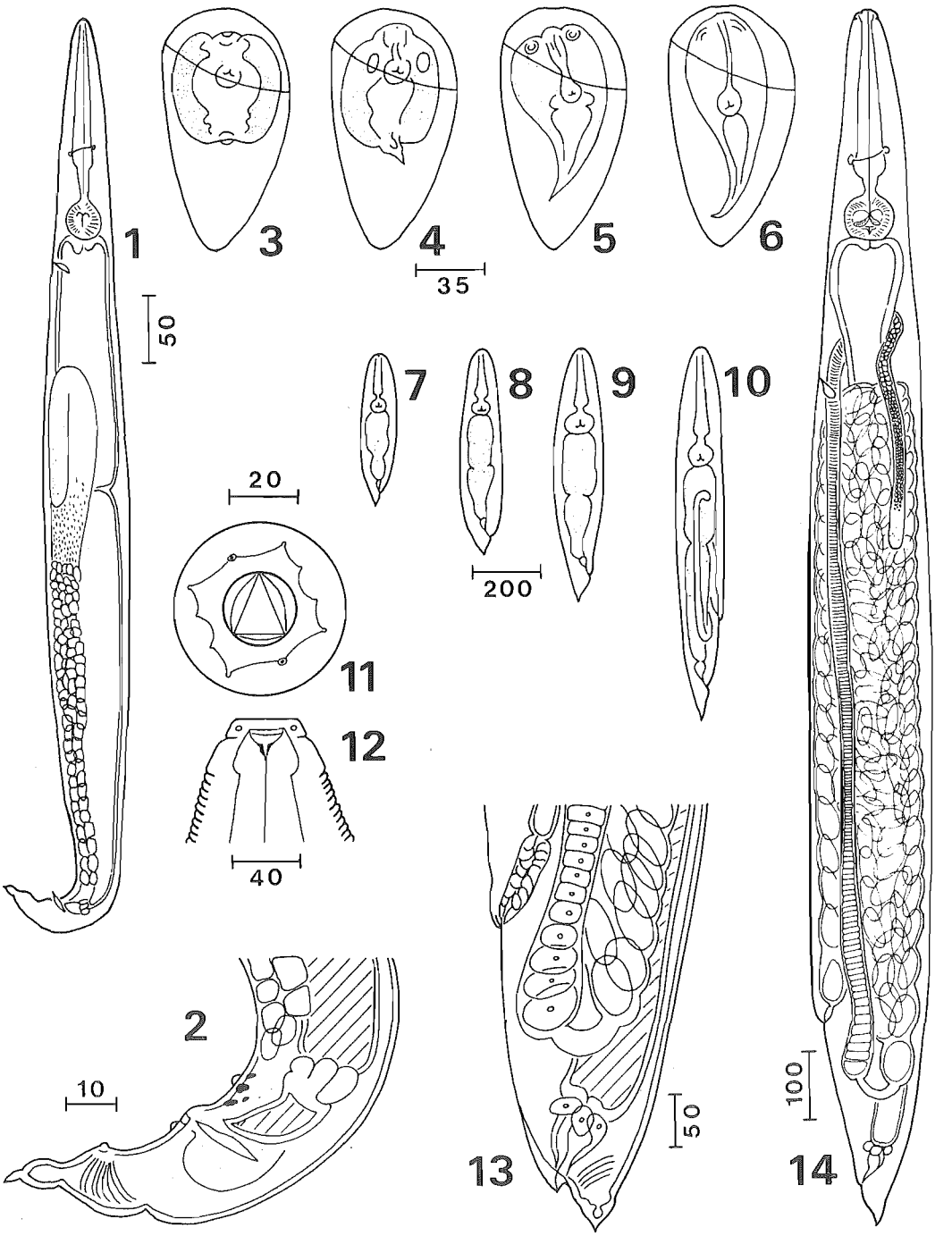
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Table 1 Dimensions (μm) of the type specimens of *Blatticola monandros* (ranges in parentheses, – = no measurement).

	Holotype female	Allotype male	Paratype females (n = 90)	Paratype males (n = 62)
Length	1985	718	1949±33 (1440–2740)	668±13 (507–920)
Width (maximum)	168	55	173±12 (160–250)	58±2 (35–70)
Width at bulb	117	41	114±7 (94–150)	44±2 (30–70)
Width at anus	66	23	54±2 (43–90)	23±1 (18–30)
Length of oesophagus	347	179	333±7 (318–347)	178±3 (120–175)
Length of corpus	242	121	295±1 (240–325)	145±2 (117–200)
Length of isthmus	39	31	38±1 (35–43)	33±1 (28–40)
Length of bulb	59	27	66±2 (60–86)	28±1 (23–38)
Width of bulb	66	27	–	–
Head to nerve ring	211	100	191±4 (270–324)	119±8 (100–125)
Head to excretory pore	507	226	550±54 (378–722)	–
Length, intestine/rectal gland junction to anus	71	–	86±3 (70–100)	–
Length of rectal glands	27	–	–	–
Length, tail to anus	66	39	66±4 (59–90)	38±1 (35–40)
Width at vulva	148	–	145±11 (129–187)	–
Head to anterior extremity of uterus	605	–	–	–
Head to anterior extremity of ovary	489	–	437±21 (350–540)	–
Tail to posterior extremity of ovary/uterus junction	190	–	215±13 (168–250)	–
Tail to vulva	293	–	299±11 (270–324)	–
Head to anterior extremity of testis	–	289	–	–
Length of spicule	–	13	–	13±1 (13–15)
Width (maximum) of spicule	–	5	–	–

Of the 2014 *P. pachycercum* collected at Kaituna Valley, 80.9% were found to harbour *B. monandros*. In smaller roach nymphs, both male and female adult nematodes were smaller, and nematode size increased with the size of the host (mean lengths: adult males 0.39 μm in size class 1 hosts, 0.67 μm in adult hosts; adult females 1350 μm in class 2 hosts, 1920 μm in adult male hosts, 1950 μm in adult female hosts). Such a relationship between host and parasite has been reported for other taxa (Christie 1931, Welch 1965). In smaller roach nymphs gravid female *B. monandros* contained few eggs, but in larger hosts females contained several hundred eggs. It is thus of apparent advantage to the female to increase in size along with the host. The similar increase in size of the

sexually mature male is more difficult to explain. Copulation was never observed in *B. monandros*, but I have observed that in *Wetanema hula* Dale, 1967, a thelastomatid from the hind gut of the indigenous weta *Hemideina thoracica* (White, 1864), the males entwine circumferentially during copulation. If *B. monandros* copulates in a similar manner, then the male may have to increase in length to compensate for increasing girth of the female.

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D) *Protrellus dixoni* N. SP. (NEMATODA: THELASTOMATIDAE) FROM THE COCKROACH *Drymaplaneta variegata*.

Abstract

Protrellus dixoni n.sp. occurs in the hind gut of the introduced Australian cockroach *Drymaplaneta variegata* in New Zealand. It is distinguished from all other species of *Protrellus* by its morphology. Females have a well developed muscular ovijector with a sphincter and a conical tail with a filiform projection; males have four, not three, tail papillae. The taxonomic history of the genus is discussed and the generic diagnosis emended. New combinations include *Protrellus eurycotesi*, *P. ischnopterae*, *P. ituana* and *P. gurri*. The population structure of *P. dixoni* in adult hosts is described: there is never more than one adult male, and usually few (1-3) adult females per host.

INTRODUCTION

Drymaplaneta variegata (Shelford, 1909) (Blattoidea: Blattidae), an Australian cockroach first recorded in New Zealand in 1954 (Hayes, 1975), is now widespread in Auckland, Gisborne and Palmerston North (Ramsay, 1975). Specimens collected from Gisborne harboured a new species of *Protrellus* (Nematoda : Thelastomatidae), which is described here. The confused taxonomic history of *Protrellus* is discussed, and the generic diagnosis emended. The population structure of the new nematode in adult hosts is outlined.

MATERIAL AND METHODS

Juvenile and adult cockroaches collected from woodpiles and outhouses on a farm at Hexton, Gisborne between June 1982 and August 1983 were identified as *Drymaplaneta variegata* by Mr. P. M. Johns,

Department of Zoology, University of Canterbury, Christchurch, New Zealand. Most cockroaches were used to establish laboratory cultures for experimental purposes (Section IV, F) and were therefore not killed. Some adult cockroaches (48 males, 23 females) were killed by crushing the nerve cord behind the head, dissected in cockroach saline, and their nematode burdens noted. Some drawings and observations were made of live nematodes in saline in wax-sealed preparations (Doncaster, 1962). Most nematodes were eventually heat-killed, fixed in TAF (triethanolamine, formalin and water, Courtney, Polley & Miller, 1955) processed using Seinhorst's (1959) glycerol/ethanol method, and mounted in anhydrous glycerine. Measurements of fixed specimens are given in μm in the text and in Table 2. Some nematodes were fixed in gluteraldehyde, post-fixed in osmium tetroxide, critical-point dried, coated with gold, and examined with a Cambridge Stereoscan 600. Images (Figs. III, D, 10-13) were recorded on 35mm film. A female was examined using a Leitz interference contrast microscope and an image (Fig, III, D, 14) similarly recorded.

RESULTS AND DISCUSSION

Superfamily Oxyuroidea

Family Thelastomatidae

Subfamily Protrelloidinae Chitwood, 1932

GENUS Protrellus Cobb: EMENDED DIAGNOSIS

Thelastomatidae; body diameter fairly uniform but tapering anteriorly and posteriorly; cuticle annulated. Females: cuticular annuli often wide anterior to vulva then flattening out to disappear posterior to oesophageal region. Mouth opening circular or triangular; eight papillae or labiopapillae; pair of small lateral amphids. Oesophagus tripartite, distinct anterior corpus with more or less swollen base separated from posterior valvular bulb by less distinct isthmus.

Figure III, D, 1-9

Protrellus dixoni from Drymaplaneta variegata.

1-5, female: (1) entire; (2) head; (3) en face; (4) ovijector; (5) excretory sinus, excretory pore (arrow 1), vulva (arrow 2), lateral view. (6) eggs. 7-9, male: (7) tail; (8) spicule; (9) entire.

(Scale lines in μm.)

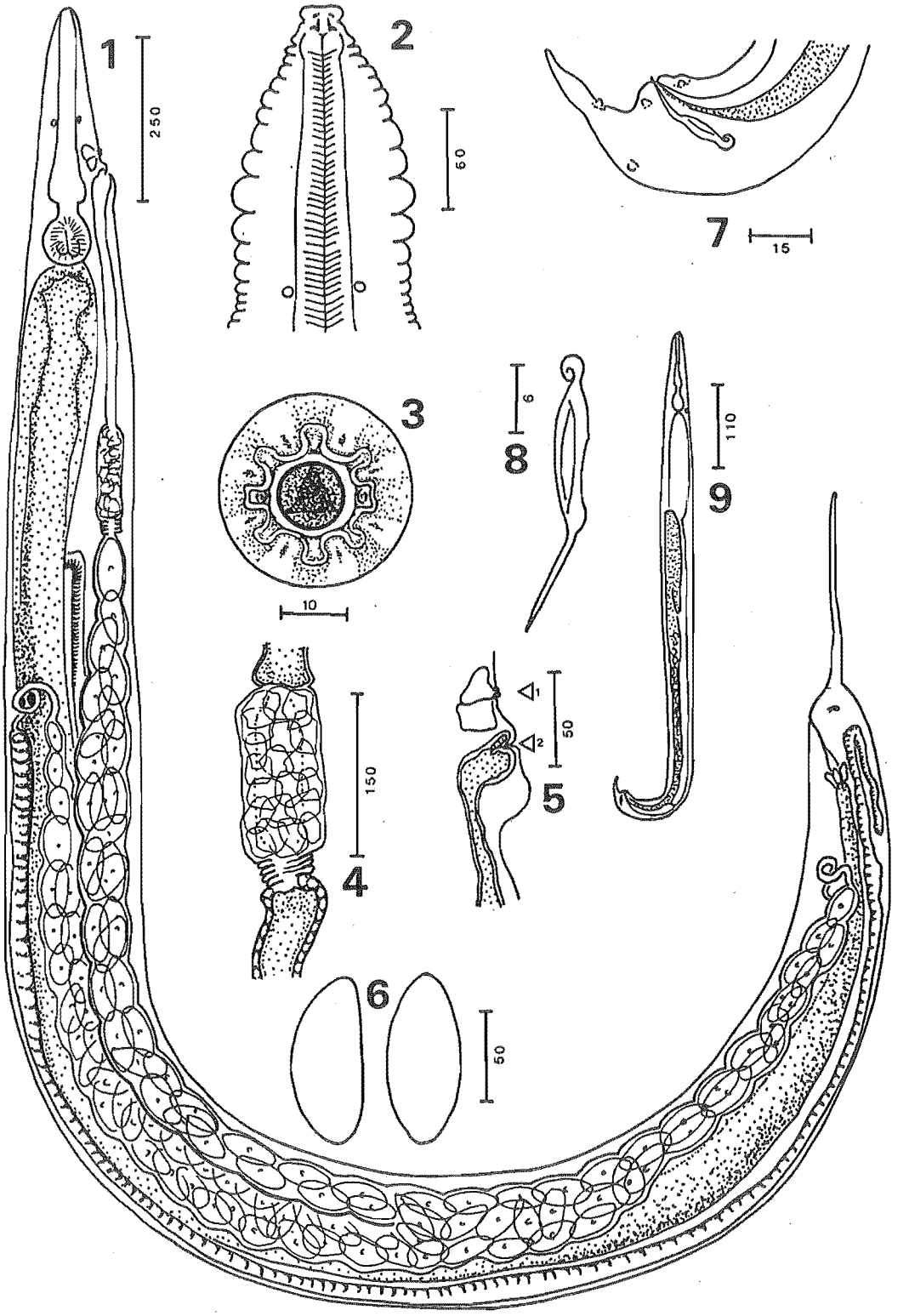

1
250
2
60
7
15
3
10
8
6
9
110
4
150
5
50
6
50

Table 2. Dimensions (µm) of the type specimens of *Protrellus dixoni* (ranges in parentheses, - = no measurement).

	Holotype female	Allotype male	Paratype females (n=13)	Paratype males (n=4)
Length	3374	725	3767±140 (2964-4758)	711±33 (612-780)
Width (maximum)	187	39	206±9 (160-269)	39±3 (31-47)
Width at bulb	144	31	144±2 (133-156)	33±2 (27-35)
Width at anus	74	15	89±3 (74±113)	15±1 (14-17)
Length of oesophagus	406	129	408±4 (375-429)	127±2 (121-133)
Length of corpus	308	-	310±4 (277-335)	-
Length of isthmus	12	-	16±1 (12-19)	-
Length of bulb	86	-	83±1 (78-90)	-
Width of bulb	78	-	79±1 (70-86)	-
Head to nerve ring	176	-	172±4 (137-195)	-
Head to excretory pore	254	132	249±3 (230-254)	130±3 (122-134)
Length intestinal/rectal gland junction to anus	133	-	124±4 (113-152)	-
Width at vulva	121	-	125±1 (117-133)	-
Head to anterior extremity of anterior ovary	838	-	863±33 (733-1236)	-
Tail to posterior extremity of posterior ovary	402	-	425±12 (359-527)	-
Head to vulva	285	-	288±3 (269-312)	-
Tail to anus	373	32	353±11 (312-429)	27±1 (24-32)
Head to anterior extremity of ovijector	632	-	682±12 (624-807)	-
Length of ovijector	148	-	173±10 (129-226)	-
Width at vulva	121	-	125±1 (117-133)	-
Head to anterior extremity of testis	-	284	-	277±14 (234-296)
Length of spicule	-	27	-	22±1 (20-27)
Egg	98x45			

Nerve ring around oesophageal corpus. Intestine expanded anteriorly; glands between intestine and rectum sometimes distinct. Excretory pore anterior to vulva. Vulva anterior to base of oesophagus. Monodelphic or didelphic. Ovijector sometimes present. Eggs oval or ellipsoidal, colourless, yellow, yellow green or yellow brown, often bearing a polar or lateral cuticular crest or boss, or lateral groove. Tail short, conical, or acutely pointed, or short cone with long filiform projection. Males: much smaller than females. Excretory pore at or beyond base of oesophagus. Testis single, reflexed or outstretched. Tail variable in shape but never plainly filiform; 2 - 4 pairs of tail papillae; one spicule. Females, males and juveniles found in hind gut of cockroaches. Geographic distribution: New South Wales, Australia; Aligarh, India; Gisborne, New Zealand; North Carolina, Maryland, U.S.A.; Brazil; Island of Madagascar.

Synonym: Protrellina Chitwood, 1932

Type species: Protrellus aureus Cobb, 1920

Protrellus dixoni n. sp. (Fig. III, D, 1-14; Table 2).

Description

Female (Fig. III, D, 1-5, 10-14). Cuticle strongly annulated only anterior to vulva; these annules (5-20 wide) greatest in width just anterior to nerve ring (Fig. 2). Lip region distinctly offset (Fig. 10). Head with circular oral opening surrounded by circular lip, then eight labiopapillae and two small amphidial apertures (Fig. 3, 10-11). Buccal capsule small, distinctly sclerotised. Oesophageal corpus sub parallel sided, slightly expanded posteriorly; isthmus distinct from corpus, but merging with bulb; bulb valve plates indistinctly sculptured. Nerve ring just over half way along corpus. Intestine broadest slightly behind oesophagus then sub parallel sided to rectum, walls thick anterior

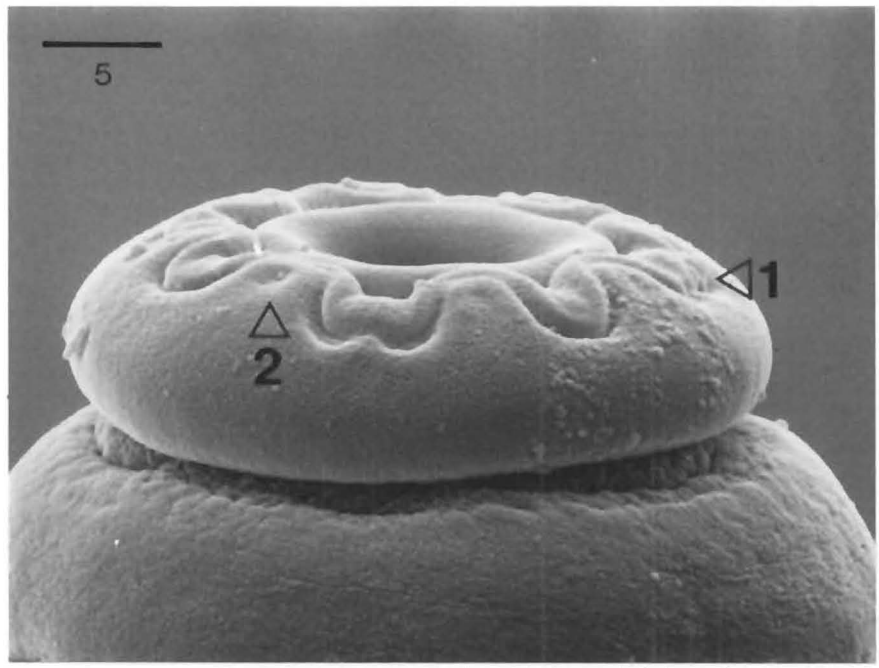
Figure III, D, 10-11

Protrellus dixoni from *Drymaplaneta variegata*.

Female head: (10) lateral view; (11) *en face*.

Amphid (arrow 1); labiopapillae (arrow 2).

(Scale lines in μm.)



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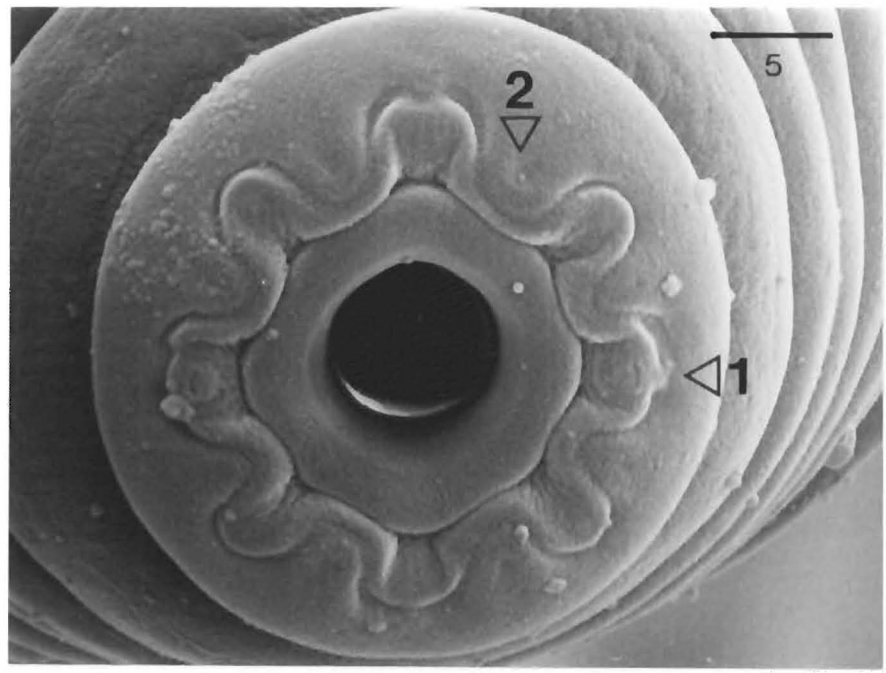

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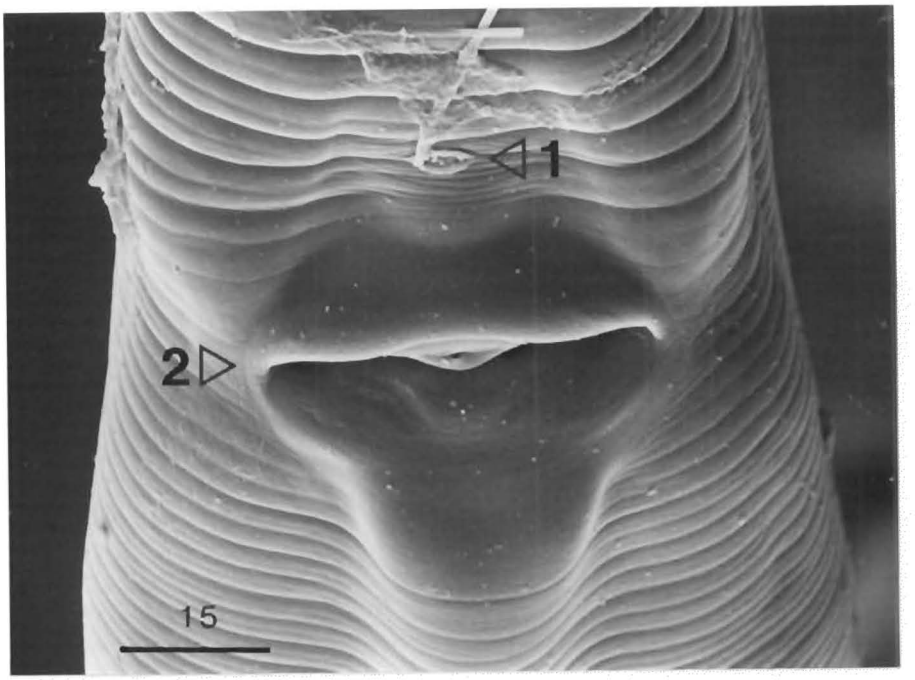
Figure III, D, 12-13

Protrellus dixoni from *Drymaplaneta variegata*.

Excretory pore lip (arrow 1); vulval lip (arrow 2).

(Scale lines in μm.)



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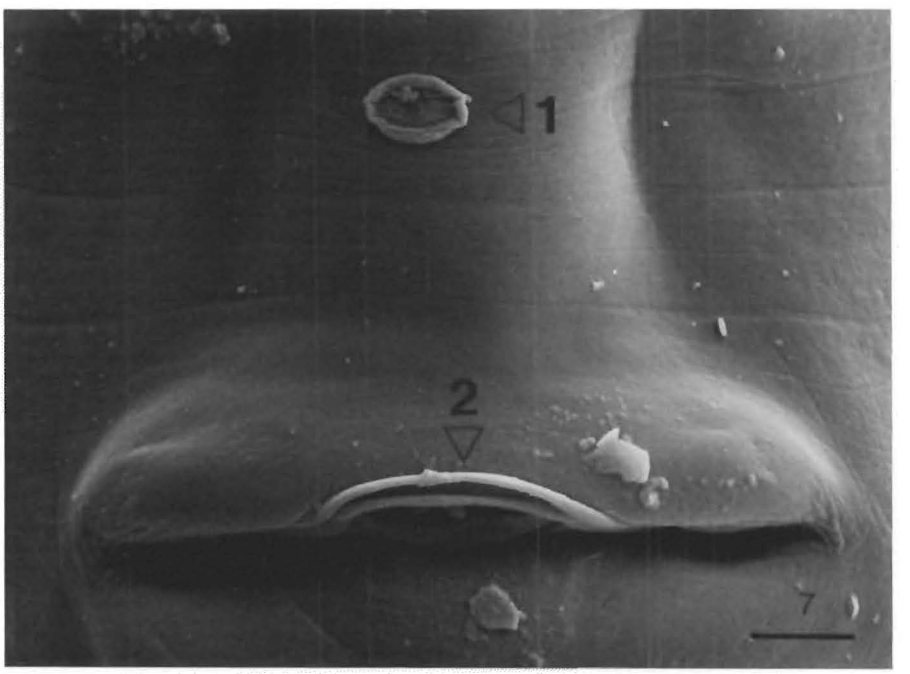

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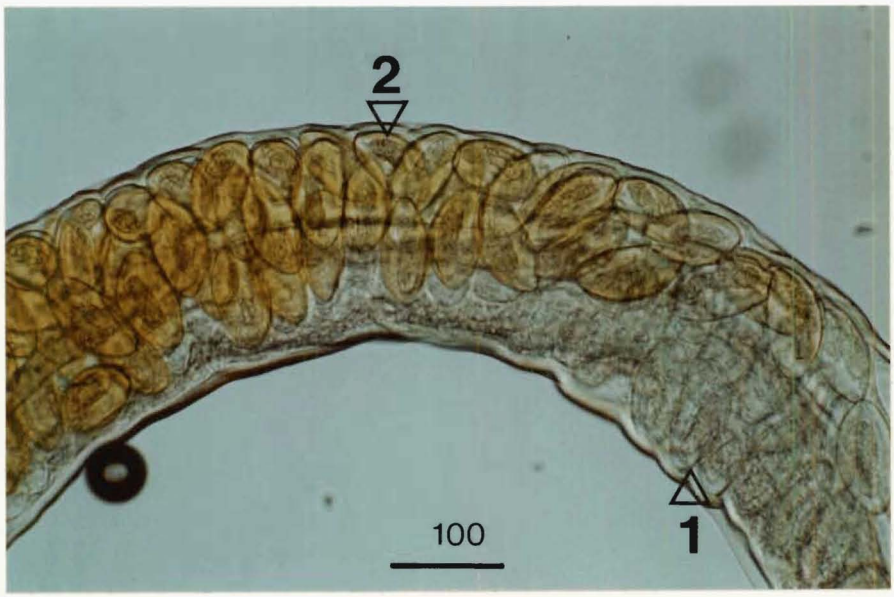

Figure III, D, 14

Protrellus dixoni from Drymaplaneta variegata.

Uterus branch with colourless eggs (arrow 1); common uterus with daffodil-yellow eggs containing infective stage juveniles (arrow 2).

(Scale line in μm.)

to anterior extremity of ovijector. Rectal glands distinct at junction of intestine and rectum. Excretory ampulla or sinus leads to excretory pore just anterior to vulva, pore surrounded by thin oval or circular rim or lip (Fig. 5, 12-13). Vulva (Fig. 12-13) in anterior tenth of body, anterior to corpus-isthmus junction (Fig. 5, 12-13) leading to thin walled vagina then thick walled, well developed, muscular ovijector with well developed posterior sphincter (Fig. 4). Reproductive system amphidelphic. Anterior and posterior branches of uterus join to form anteriorly directed common uterus near middle of body. Posterior branch arises from an oviduct coiled several times in posterior quarter of body before receiving anterior ovary, this ovary reflexed in region of uterus-ovijector junction. Anterior branch arises from a coiled oviduct which receives the posterior ovary; this ovary directed posteriad then reflexed in region of rectum to pass anteriad for a short distance. Eggs (Fig. 6, 14) oval, rounded at one end, slightly pointed at the other, one side slightly flattened in lateral view, surface punctate, shell of fairly uniform thickness throughout, colourless in branches of uterus, but daffodil-yellow in common uterus (Fig. 14). Amoebocytes large, visible in posterior half of pseudocoelom in some living specimens. Tail conical, with long filiform projection; pair of phasmids in conical region, phasmidial duct sometimes visible.

Male (Fig. III, D, 7-9). Very small compared to female. Cuticle annulated over entire body (annules about 1 wide). Lip indistinct; amphidial apertures and labial papillae, not seen. Oesophageal regions indistinct. Nerve ring not seen. Intestine broadest behind oesophagus then sub parallel sided to cloaca. Excretory pore just posterior to oesophagus or level with its posterior end. Glands between intestine and cloaca conspicuous in life. Testis extends anteriad, then reflexed posteriorly at 40% of body length from anterior end. Spicule small,

round at proximal end, narrow neck leading to broad middle part, then narrowing distally to form a long acute point; without capitulum. No gubernaculum. Four pairs of tail papillae, three pairs ventro-lateral (one pair pre-anal, two pairs post-anal), one pair dorso-lateral. Tail rounded, with short filiform projection.

Juveniles. Juvenile males distinguished from juvenile females by the possession of a fully developed spicule (but no testis) and a short (not long) filiform projection on tail cone.

Type data. Holotype female, allotype male and 17 paratypes (13 female, 4 male) in New Zealand National Nematode Collection, Entomology Division, Department of Scientific and Industrial Research, Auckland (holotype female, NZNNC holotype no. 124; allotype male, NZNNC 125; 13 paratype females, NZNNC 2118-2130; 4 paratype males NZNNC 2131-2134).

Type host: Drymaplaneta variegata (Shelford, 1909). Site in host: anterior end of colon of hind gut.

Type locality: Hexton, Gisborne, North Island, New Zealand (38° 37' 0"S, 177° 58' 20"E); elevation 100m; 14/6/1982.

Remarks: The species is named for Ms. Mary Dixon, who collected the hosts.

TAXONOMY

The genus Protrellus was proposed by Cobb (1920) for P. aureus, a thelastomatid with a short conical tail from an Australian cockroach, Polyzosteria sp.. Schwenck (1926) described P. galebi from another (unnamed) cockroach. Travassos (1929) transferred Oxyuris kunckeli Galeb, 1878 and O. australasiae Pessoa & Correa, 1926 to Protrellus. In 1932, Chitwood created three new genera (Protrelloides,

Protrelleta and Protellina) in a new subfamily (Protrelloidinae) based on the position of the vulva anterior to the oesophagus. Chitwood (1932) transferred P. galebi, P. kunckeli and P. australasiae to Protrellina and added 2 new species, P. manni and P. aurifluus. He regarded Cobb's P. aureus as a species inquirenda and did not recognise Protrellus as a valid genus. Later (1933), Chitwood considered that Protrellus and Protrellina were identical and reinstated the senior name for the genus. Basir (1942) described Protrellina phyllodromi from a cockroach but later (1956) reduced this genus to a synonym of Protrellus. Basir (1956) also abolished Chitwood's (1932) subfamily Protrelloidinae on the grounds that the position of the vulva is variable in thelastomatids and is not a distinct enough character on which to erect a subfamily. Kloss (1961, 1966) and Dale (1966), apparently unaware of Chitwood's (1933) paper described new thelastomatids in the genus Protrellina (P. eurycotesi Kloss, 1961; P. ischnopterae Kloss, 1966; P. ituana Kloss, 1966 and P. gurri Dale, 1966). Van Waerebeke however (1969), used the name Protrellus, in a description of two new species, P. rasolofi and P. behorefi. Farooqui, in a review paper (1970), resurrected Chitwood's subfamily Protrelloidinae in which he included Protrelloides Chitwood, 1932, Protrellata, Chitwood, 1932, and Protrellus Cobb, 1920, and to which he assigned a new genus, Protrellatus. Thus he and later authors (eg., Poinar, 1975) used the senior name for the genus. In my opinion, Cobb's original (1920) generic name Protrellus, and Chitwood's (1932) subfamily Protrelloidinae, are valid. Protrellina eurycotesi Kloss, 1961, P. ischnopterae Kloss, 1966, P. ituana Kloss, 1966, and P. gurri Dale, 1966, are assigned to the genus Protrellus as new combinations.

Cobb's original generic diagnosis, and diagnoses of later authors (eg. Basir, 1956) describe the female tail as short, conical, never filiform and the male tail as having 2-3 papillae. Dale (1966) and Van Waerebeke (1969) described females of new species (*P. gurri* and *P. rasolofi* respectively) with long filiform tails but did not refer to the diagnostic restriction on tail length. *P. dixoni* females also have a filiform tail. Dale (1966) noted that *P. gurri* males differed from other species in the genus in having 4 tail papillae, but did not comment on the original generic diagnosis of 2-3 papillae. *P. dixoni* males also have 4 tail papillae. The emended diagnosis of the genus given earlier was modified to accommodate *P. dixoni* and species described after 1960.

DIFFERENTIAL DIAGNOSIS OF *Protrellus dixoni*

P. dixoni females have a suite of characters that distinguish them from other species of *Protrellus* (Appendix 1) that include: broad and narrow cuticular annules anterior to the vulva (as have *P. galebi*, *P. manni*, *P. eurycotesi*, *P. gurri* and *P. rasolofi* but not others, which have uniform striations over the entire body, only uniform striations anterior to the vulva, or striations not described or figured); anterior thickening of the intestine wall (as has *P. ituana* but not others, which have a fold in the anterior wall of the intestine or intestine walls of uniform thickness throughout); a lipped excretory pore (as have *P. rasolofi* and *P. behorefi* but not others, which have a simple or slightly indented pore, or pore not described or figured); a muscular ovijector with posterior sphincter (*P. galebi* and *P. eurycotesi* have an ovijector, but sphincter not mentioned); a posterior ovary which is reflexed in the region of the rectum (as have *P. rasolofi* and *P. aurifluus* but not others, which have an ovary reflexed anterior to the rectum, or a plainly outstretched ovary - the

exception is P. australasiae, which differs from all others in being monodelphic); a round tail with a long filiform projection (as have P. gurri and P. rasolofi but not others, which have convex conoid, or acutely pointed tails); and large, plainly oval, daffodil-yellow eggs (others have crests, bosses or grooves, and/or are not daffodill-yellow in colour).

Males: comparison of Protrellus species males is hindered because for half of all species described, males are unknown. Of those known, P. dixoni have average dimensions (Appendix 2) but differ from all except P. gurri in having four pairs of tail papillae. They differ from P. gurri in being larger overall and in the acutely angled spicule (spicule almost straight in P. gurri).

POPULATION STRUCTURE

Adult and juvenile Protrellus dixoni were found in the anterior part (colon) of the hind gut. A few juveniles ($n = 6$) could not be sexed and are here ignored. Infection prevalence was 55% (58% of male and 52% of female cockroaches were infected). This is low compared to infection prevalence of Blatticola monandros Zervos, 1983 (81%, Section III, C), the only other thelastomatid for which infection data in wild hosts (Parellipsidion pachycercum Johns, 1966) are available. No host had more than one adult male, and the number of adult females/host was usually small. Over half (52.5%) of infected cockroaches had either 1:1 (35%), 1:2 (10%), or 1:3 (7.5%) adult male to adult female nematodes. Sometimes, a male was accompanied by juvenile females, or both juvenile and adult females. Amongst hosts with no male, some had either adult females only or juvenile females only, or both. Usually, juvenile females were more numerous in a host (up to 23) if adult females were scarce or absent. Only one host had a juvenile male (together with 20

juvenile females). Thus P. dixoni resembles B. monandros in that never more than one adult male is found per host, and the number of adult females present is usually small (Section III, C).

As a parasite, P. dixoni is probably benign as no host appeared damaged. The presence of both juvenile and adult nematodes in hosts, and experimental evidence (Section IV, F), indicates that P. dixoni has a direct life cycle, as do other thelastomatids (Dobrovolny & Ackert, 1934; Poinar, 1975; Todd, 1944; Welch, 1963). Within the host, adult females were either outstretched with the head anteriorly directed or were reflexed, with both head and tail anteriorly directed. The male occurred anterior to the female(s) or alongside the head of the anterior-most female. Juvenile nematodes were apparently randomly distributed anteriorly. In their precocial development, juvenile male P. dixoni resemble B. monandros males, which are also precocial (Section III, C), as are probably all oxyurids (Adamson, 1981b, 1983; Jarry, 1964).

E) *Protrellus dalei* N. SP., *Blatticola barryi* N. SP., AND *Suifunema mackenziei* N. SP., THELASTOMATID NEMATODES FROM NEW ZEALAND COCKROACHES.

Abstract

Three new species of thelastomatid nematode from the hind guts of New Zealand cockroaches are described. They are *Protrellus dalei* n.sp. from *Celatoblatta vulgaris*, *C. peninsularis* and *C. brunni*; *Blatticola barryi* n.sp. from *C. quinquemaculata*; and *Suifunema mackenziei* n.sp. from *C. undulivitta*. This is the first record of *Suifunema* in New Zealand. The diagnoses of the genera *Blatticola* and *Suifunema* are emended to accommodate the new species. Keys to species of *Protrellus* and *Blatticola* are given and the larval development of *P. dalei* is discussed. Aspects of the biology and distribution of the new species are noted.

INTRODUCTION

Thelastomatids (Nematoda: Thelastomatidae) live in the alimentary canals of a variety of detritivorous, coprophagous, and saprophagous arthropods. Most of the nearly two hundred described species are from cockroaches. Of these, only four are from New Zealand. *Blatticola tuapakae* Dale, 1966 and *Protrellus gurri* (Dale, 1966) Zervos, 1986 (Section III, D) occur in *Platyzosteria novaeseelandia* Brunner, 1856 (but not together), while *Blatticola monandros* Zervos, 1983 (Section III, C) occurs in *Parellipsidion pachycercum* Johns, 1966. The introduced Australian cockroach *Drymaplaneta variegata* (Shelford, 1909) also has a thelastomatid, *Protrellus dixoni* Zervos, 1986 (Section III, D). Recently, three undescribed species of thelastomatid were found in several species of native cockroach from numerous collection sites.

These thelastomatids are described here and belong in Protrellus, Blatticola, and Suifunema. The diagnoses of the genera Blatticola and Suifunema are emended to accommodate the new species, and keys to species of Protrellus and Blatticola are given.

MATERIAL AND METHODS

Cockroaches were collected during 1981-1984 from habitats at the locations indicated in the following descriptions. They were killed by crushing the nerve cord behind the head and dissected in cockroach saline. Some drawings and observations were made of live nematodes in saline in wax-sealed preparations (Doncaster, 1962). Most nematodes were eventually heat-killed, fixed in TAF (Courtney et al., 1955), processed using Seinhorst's (1959) glycerol/ethanol method, and mounted in anhydrous glycerine. Measurements of fixed specimens are given in µm in Tables 3-5 and in the text. Adult nematodes are described from adult hosts only. Some differential comparisons of the new species are based on my own calculations of dimensions from figures or tables accompanying descriptions of existing species. Some nematodes were fixed in gluteraldehyde, post-fixed in osmium tetroxide, critical-point dried, coated with gold, and examined with a Cambridge Stereoscan 600. Images (Figs. III, E, 11-12, 14) were recorded on 35mm film. Some nematodes were examined using a Leitz interference contrast microscope and images (Figs. III, E, 10, 13, 15-17, 29-30) similarly recorded.

DESCRIPTIONS

Superfamily Oxyuroidea

Family Thelastomatidae

Subfamily Protrelloidinae Chitwood, 1932

GENUS *Protrellus* COBB, 1920

Synonym: *Protrellina* Chitwood, 1932

DIAGNOSIS (EMENDED)

Thelastomatidae; body diameter fairly uniform but tapering anteriorly and posteriorly; cuticle annulated. Females: cuticular annuli often wide anterior to vulva then flattening out to disappear posterior to oesophageal region. Mouth opening circular or triangular; eight papillae or labiopapillae; pair of small lateral amphids. Oesophagus tripartite, distinct anterior corpus with more or less swollen base separated from posterior valvular bulb by less distinct isthmus. Nerve ring around oesophageal corpus. Intestine expanded anteriorly; glands between intestine and rectum sometimes distinct. Excretory pore anterior to vulva. Vulva anterior to base of oesophagus. Monodelphic or didelphic. Ovijector sometimes present. Eggs oval or ellipsoidal, colourless, yellow, yellow green or yellow brown, often bearing a polar or lateral cuticular crest or boss, or with a lateral groove. Tail short, conical, or acutely pointed, or short cone with long filiform projection. Males: much smaller than females. Excretory pore at or posterior to base of oesophagus. Testis single, reflexed or outstretched. Tail variable in shape but never plainly filiform; 2 - 4 pairs of tail papillae; one spicule.

Females, males and juveniles found in hind gut of cockroaches.

Geographic distribution: New South Wales, Australia; New Zealand; North Carolina, Maryland, U.S.A.; Island of Madagascar; Brazil; Aligarh, India.

Type species: *Protrellus aureus* Cobb, 1920

Protrellus dalei n. sp. (Fig. III, E, 1-17, Table 3).

Description

Females (Fig. III, E, 3-8, 10-13) Cuticle strongly annulated only anterior to vulva; first annule 12, subsequent annules 6 wide; annules indistinct posterior to base of oesophagus. Lip region offset (Fig. 4). Head with circular oral opening surrounded by circular lip, then eight very small papillae and two small, oval amphidial apertures (Fig. 8). Buccal capsule small, distinctly sclerotised, width 6-8. Oesophageal corpus sub-parallel sided, slightly expanded posteriad; isthmus distinct from corpus but merging with bulb; bulb valve plates indistinctly sculptured. Nerve ring just over half way along corpus. Intestine broadest slightly behind oesophagus, decreasing in diameter at level of anterior extremity of anterior ovary, then subparallel sided to rectum. Rectal glands distinct at junction of intestine and rectum. Excretory ampulla or sinus leads to excretory pore just anterior to vulva (Fig. 10); pore surrounded by broad, flat, circular lip (Fig. 11-12). Vulva in anterior tenth of body, just anterior to corpus-isthmus junction, leading to thin walled vagina then poorly developed muscular ovijector in region of anterior extremity of ovary. Reproductive system amphidelphic. Anterior and posterior branches of uterus join to form anteriorly directed common uterus near middle of body; this common uterus with ovijector (Fig. 13). Posterior branch arising from an oviduct coiled several times in posterior quarter of body; this arising from an anterior ovary reflexed in region of narrowing of intestine to pass posteriad for a short distance. Anterior branch arising from a coiled oviduct which arises in turn from an ovary reflexed in region of narrowing of intestine, this ovary originating posteriorly, near junction of uteri. Eggs (Fig. 9, 13-14) oval; slightly broader at one end, shell thickened slightly at both ends, more so at pointed end;

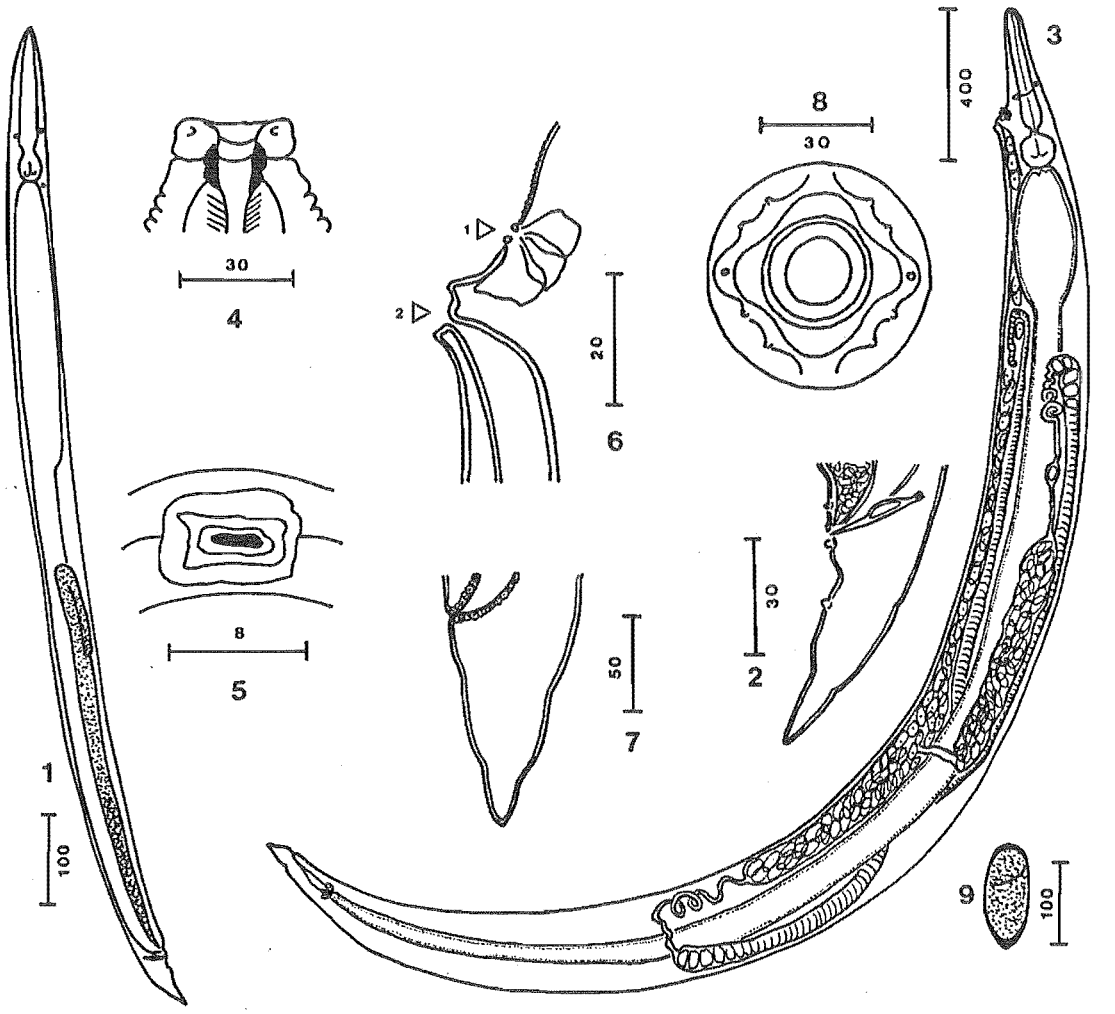

Figure III, E, 1-9

Protrellus dalei from Celatoblatta vulgaris, C. peninsularis and C. brunni.

1-2, male: (1) entire; (2) tail. 3-8, female: (3) entire; (4) head; (5) excretory pore lip; (6) excretory sinus, excretory pore (arrow 1), vulva (arrow 2), lateral view; (7) tail; (8) en face. (9) egg.

(Scale lines in μm.)

Table 3. Dimensions (μm) of the type specimens of Protrellus dalei (ranges in parentheses, - = no measurement).

	Holotype female	Allotype male	Paratype females (n=12)	Paratype males (n=12)
Length	4400	1148	4166±135 (2980-4900)	1007±27 (840-1148)
Width (maximum)	250	56	213±14 (130-310)	49±2 (40-68)
Width at bulb	180	40	177±8 (110-220)	38±1 (30-52)
Width at anus	60	24	77±4 (60-100)	22±1 (16-30)
Length of oesophagus	440	180	414±5 (360-440)	155±3 (124-180)
Length of corpus	340	-	309±5 (260-340)	-
Length of isthmus	24	-	25±1 (20-32)	-
Length of bulb	76	36	79±2 (68-90)	31±2 (20-56)
Width of bulb	80	-	75±2	(64-88)
Head to nerve ring	190	110	169±4 (140-188)	85±9 (84-120)
Head to excretory pore	290	200	244±6 (220-290)	188±5 (168 220)
Length intestinal/rectal gland junction to anus	200	-	163±7 (120-200)	-
Head to anterior extremity of anterior ovary	770	-	734±43 (500-1200)	-
Tail to posterior extremity of posterior ovary	1200	-	996±59 (780-1560)	-
Head to vulva	300	-	273±5 (260-320)	-
Tail to anus	100	60	106±3 (90-128)	71±2 (56-110)
Length tail to posterior-most papillae	-	42	-	42±2 (36-50)
Head to anterior extremity of testis	-	570	-	498±24 (360-750)
Length of spicule	-	24	-	26±6 (20-28)
Egg	98x45			

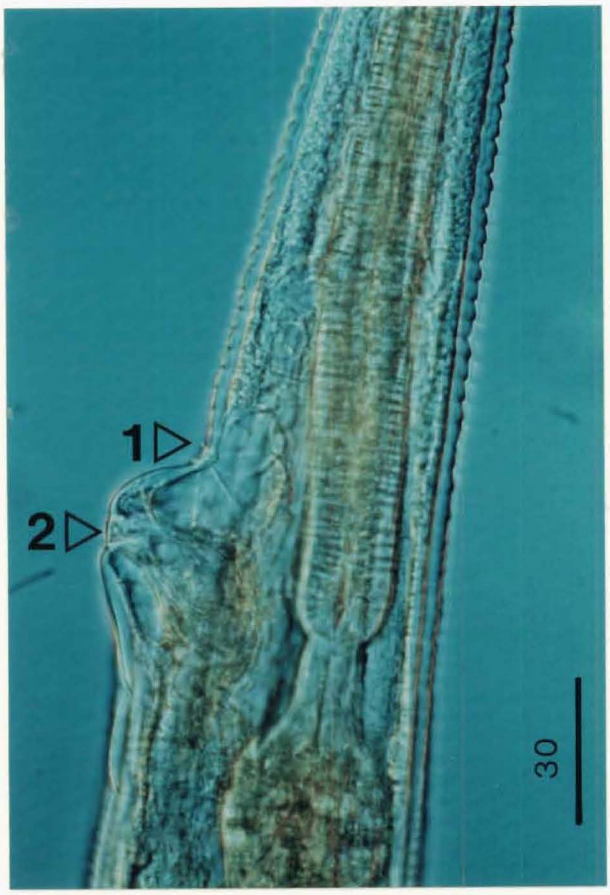

Figure III, E, 10

Female Protrellus dalei from Celatoblatta peninsularis.

Excretory pore, excretory sinus (arrow 1); vulva (arrow 2).

(Scale line in μm).

Figure III, E, 11-12

Female *Protrellus dalei* from *Celatoblatta peninsularis*.

Excretory pore lip (arrow 1); vulval lip (arrow 2).

(Scale lines in μm.)

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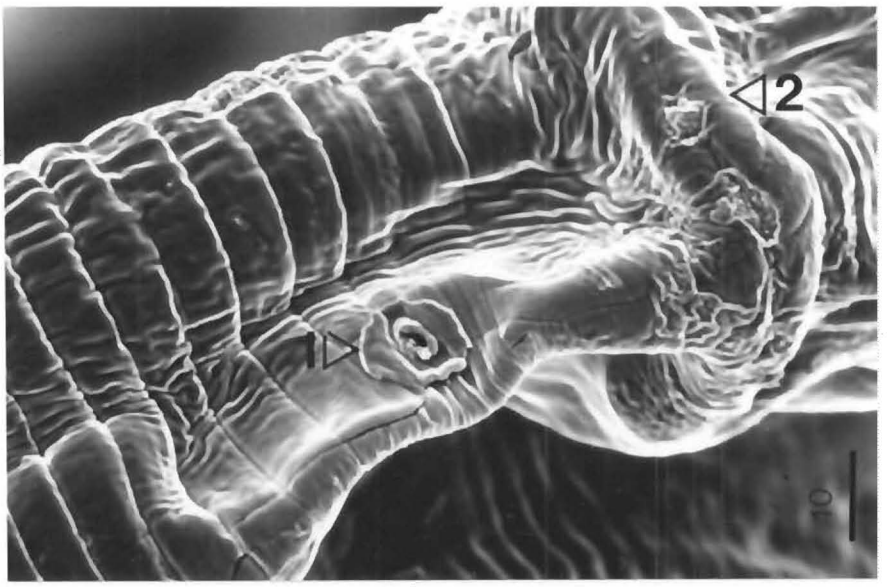

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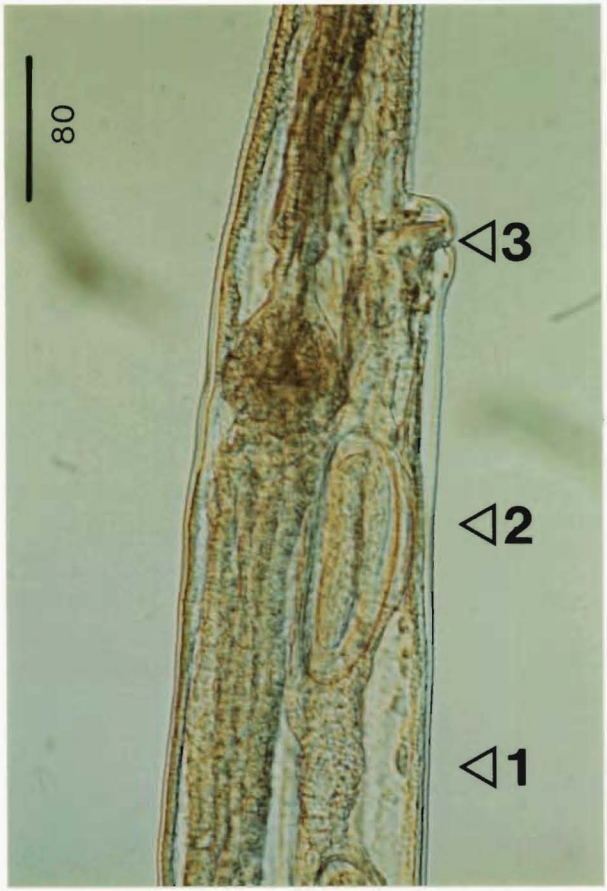


Figure III, E, 13

Protrellus dalei from Celatoblatta peninsularis

Female with egg containing active form juvenile (arrow 2). Ovijector (arrow 1); vulva (arrow 3).

(Scale line in μm.)

Figure III, E, 14-15

Protrellus dalei from Celatoblatta peninsularis.

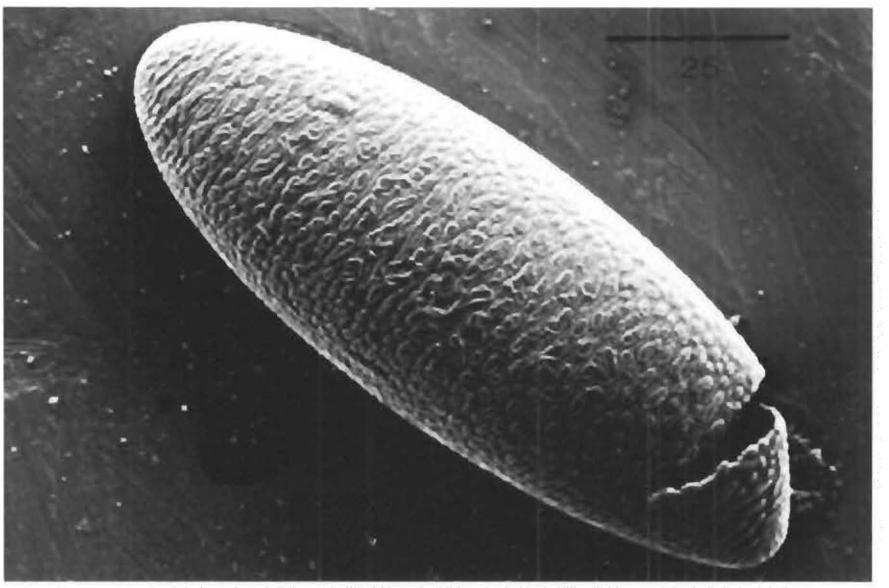
Eggs and juveniles.

14, egg showing punctate surface and opercular cap.

15, pre-infective form juveniles released through operculum of eggs by pressure on cover slip.

Oesophageal bulb (arrow 1); coiled intestine (arrow 2).

(Scale lines in μm.)



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surface punctate; with operculum; colourless. Tail very short, conical, formed of two or three indistinct convex conoids of diminishing size, cuticle of tail tip not thickened.

Males (Fig. III, E, 1-2, 17). Much smaller than females. Cuticle not distinctly annulated. Lip slightly offset; amphidial apertures and labial papillae not seen. Oesophageal regions barely distinguishable. Nerve ring just anterior to corpus-isthmus junction. Intestine subparallel sided, constricted somewhat near middle in live specimens. Excretory pore just posterior to oesophagus (not seen in all specimens). Glands between intestine and cloaca conspicuous in life. Testis extends anteriad, then reflexed posteriad posterior to mid body point. Spicule small, rounded proximally, broadest at the middle, tapering to a point distally; without capitulum. No gubernaculum. Three pairs of latero-ventral papillae; one pair pre-anal, two pairs post-anal. Tail a tapering cone with ventral constriction.

Juveniles in eggs. Embryos in eggs developed into active juveniles with bodies longer than the egg shell (Fig. 13); such juveniles were reflexed. Juveniles then shrank to about 2/3 the length of the shell. They remained in this state thereafter.

Juvenile females. L2 (n= 15). Length (L)= 226 +/- 5 (Range, R.= 215-312); maximum width (W. max.)= 23 +/- 2 (R= 21-25). Cuticle not distinctly annulated. Lips indistinct. Oesophagus (L= 100 +/- 9, R= 87-112) as in adult female but extending 44% of body length. Oesophageal bulb valvate, with indistinctly sculptured plates. Intestine as in adults. Excretory pore not evident. Tail short, conical.

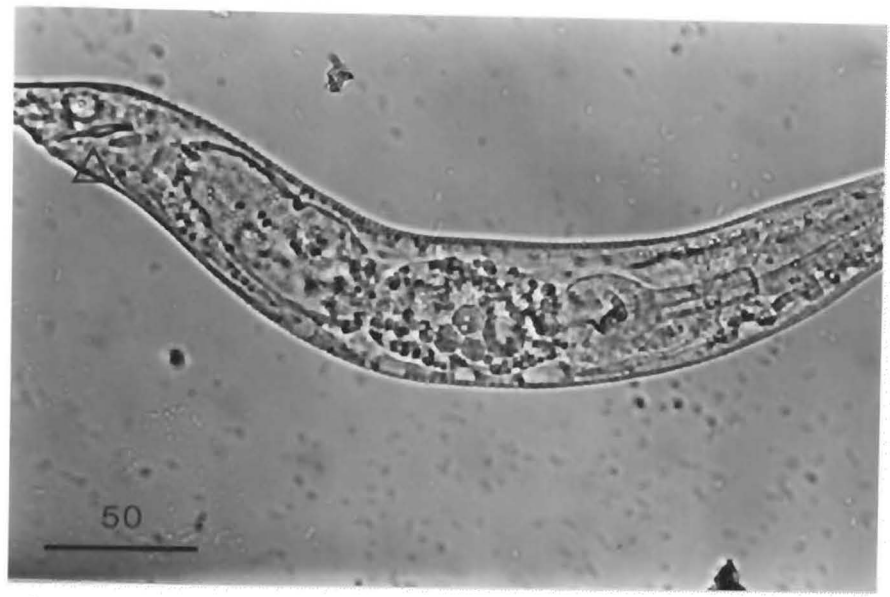
Figure III, E, 16-17

Male *Protrellus dalei* from *Celatoblatta peninsularis*.

16, juvenile with spicule (arrow) but no testis.

17, adult with spicule and testis (arrow).

(Scale lines in μm.)



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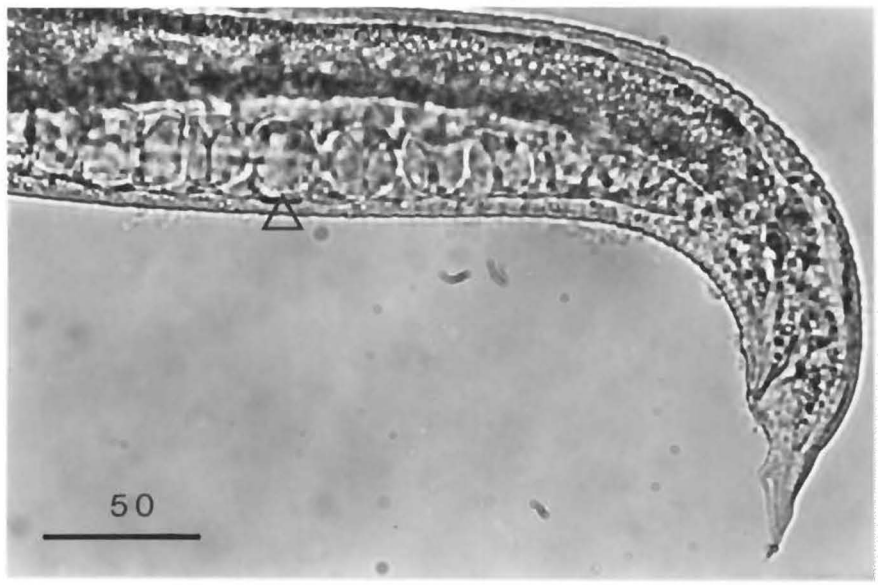

17

L3 (n= 11). L= 520 +/- 15 (R= 440-590); W.max.= 43+/- 5 (R= 39-59). Cuticle distinctly annulated. Lips distinct, offset. Oesophagus (L= 160+/- 11; R= 149-168) as in adult female but extending 33% of body length. Intestine broad anterior to distinct intestinal constriction, then subparallel sided to rectum. Excretory pore and small excretory sinus evident just anterior to oesophageal bulb. Nerve ring distinct, encircles corpus. Tail (L= 40 +/-5; R= 38-45) short, conical.

L4 (n= 6). L= 1570 +/- 98 (R= 970-2014); W. max.= 98 +/- 14 (R= 84-113). Cuticle distinctly annulated; lips distinctly offset. Oesophagus (L= 370 +/- 47; R= 250-393) as in adult female but extending 24% of body length. Intestine as in L3. Excretory pore and well developed sinus at level of isthmus; developing vulva just posterior to this. Developing reproductive system evident. Tail (L= 90 +/- 10; R= 78-111) conical.

Juvenile males (Fig. 16): juvenile males were rare, but could be distinguished from juvenile females and adult males by their small size, by their possession of a spicule and adult like tail, but absence of gonad (Fig. 16-17).

Type data. Holotype female, allotype male and 18 paratypes (9 female, 9 male) in New Zealand National Nematode Collection, Entomology Division, Department of Scientific and Industrial Research, Auckland (holotype female, NZNNC holotype no. XXX; allotype male, NZNNC XXXX; 9 paratype females, NZNNC XXXX-XX; 9 paratype males NZNNC XXXX-XX).

Type host: Celatoblatta vulgaris Johns, 1966. Site in host: anterior end of colon of hind gut. Other hosts: C. peninsularis, C. brunni.

Type locality: Castle Hill, Canterbury, South Island, New Zealand (43° 13' 20"S, 171° 42' 40"E); elevation 500m; 9/10/1983. Other localities: Mount White, Craigieburn, Maruia Springs, Reefton, Cass, Klondyke Corner, Charming Creek, Kaituna Valley (South Island, New Zealand); Tuku Valley (Chatham Island Group, New Zealand).

Remarks: The species is named for the New Zealand nematologist and entomologist, Mr. Pat Dale.

Differential diagnosis of Protrellus dalei

Females: P. dalei are unique in possessing a suite of characters (Appendix 1) that include: anterior annules (excluding the first) of almost uniform width (as have others except P. galebi Schwenck, 1926, P. aureus Cobb, 1920, P. dixoni Zervos, 1986 (Section III, D) and P. manni (Chitwood, 1932) Chitwood, 1933, which have broad and narrow anterior annules); a distinct oesophageal isthmus (merging in others); a lipped excretory pore (as have P. dixoni, P. rasolofi Van Waerebeke, 1969 and P. behorefi Van Waerebeke, 1969 but not others); a posterior ovary reflexed anterior to the rectum (as have others except P. rasolofi and P. aurifluus (Chitwood, 1932) Chitwood, 1933 and P. australasiae (Pessoa & Correa, 1926) Travassos, 1929, which have a posterior ovary reflexed in the region of the rectum); a short tail composed of diminishing convex conoids (as has P. behorefi but not others, in which the tail is plainly conical, or subulate (P. ituana (Kloss, 1966) Zervos, 1986; Section III, D) or with constrictions (P. manni), or filiform projections (P. gurri, P. dixoni and P. rasolofi); an ovijector (as have P. dixoni, P. ituana, P.eurycotesi (Kloss, 1961) Zervos, 1986 (Section III, D), P. galebi,

and P. ischnopterae (Kloss, 1966), Zervos, 1986 (Section III, D), but not others); this ovijector not well developed and apparently lacking a sphincter (ovijector muscular, with sphincter in P. dixoni, sphincter not noted in others).

P. dalei eggs are quite large (137x51), but not as large (150x85) as those of P. kunckeli (Galeb, 1878), Travassos, 1929 and are colourless, plainly oval, and without the bumps, grooves or crests of others.

Males: comparison of Protrellus species males is hindered because for half of the species, males are unknown. Of those known, P. dalei have greatest body length (Appendix 2), the longest tail, and 3 pairs of tail papillae (as have others except P. dixoni and P. gurri, which have 4 pairs).

Larval P. dalei: Although larval females increase in overall length and width with each successive stage, the ratio of oesophageal length to total body length decreases. Total female body length (from L2 to adult) increases 17 fold while oesophageal length increases only 4 fold. Such allometric growth is common amongst nematodes (for example, see Yeates, 1973).

The confused taxonomic history of the genus Protrellus was clarified in Section III, D. As a key to the species in the genus Protrellus has not appeared for over 30 years (the last in Basir, 1956), and as over half the known species in the genus have been described since that key was published, a new key is provided.

KEY TO SPECIES IN THE GENUS *Protrellus*

1. - Female tail conical, with long filiform projection.....2

   - Female tail short, no filiform projection.....4

2. - Female: excretory pore without lip; posterior ovary reflexed anterior to rectum, about one third of a body length from posterior end; egg ovoid with crest; male: tail shorter than spicule.....*P. gurri* (Dale, 1966) Zervos, 1986 (Section III, D)

   - Female: excretory pore with lip; posterior ovary reflexed at or posterior to rectum; egg ovoid without crest; male: tail longer than spicule.....3

3. - Female: 2964-4758 long; cuticular annulations broad and narrow anterior to vulva; excretory pore with thin circular or oval lip; mouth circular; muscular ovijector; egg 98 x 45; male: 4 pairs of tail papillae.....*P. dixoni* Zervos, 1986 (Section III, D)

   - Female: 5600-7660 long; cuticular annulations more or less uniform anterior to vulva; excretory pore covered by flap; mouth subtriangular; no ovijector; egg 65-73 x 38-45; male : 3 pairs of tail papillae.....*P. rasolofi* Van Waerebeke, 1969

4. - Egg with crest or bosses.....5

- Egg without crest or bosses.....10

5. - Female oesophagus >600; vulva in region of oesophageal bulb; egg 130-180 x 70-100; male: >800; spicule 50.....*P. kunckeli* (Galeb, 1878) Travassos, 1929

- Female: oesophagus <510; vulva anterior to oesophageal bulb; egg <100 x 50; male (where known): <300), spicule <20.....6

6. - Female: 8585-10370; excretory pore not evident; vulva not salient; with ovijector .....*P. eurycotesi* (Kloss, 1961) Zervos, 1986 (Section III, D)

- Female: <4500; excretory pore evident or not; vulva salient; with or without ovijector.....7

7. - Female: 3400-5200; tail plainly conical.....8

- Female: <2750; tail with small appendix or pronounced constriction.....9

8. - Female: 4120 long; tail 54; vulva about half way along oesophageal corpus; excretory pore not evident; posterior ovary reflexed twice anterior to rectum; egg crest reduced.....*P. ischnopterae* (Kloss, 1966) Zervos, 1986 (Section III, D)

- Female: 3400-5200 long; tail 100-290; vulva near base of oesophageal corpus; excretory pore evident; posterior ovary reflexed once in region of rectum; egg crest prominent.....P. aurifluus (Chitwood, 1932) Chitwood, 1933

9. - Female: 2620 long; tail with medial constriction; excretory pore evident; oesophageal corpus bent before union with isthmus; vulva near posterior end of corpus; two ovaries; lateral crest of egg with cuticular bosses.....P. manni (Chitwood, 1932) Chitwood, 1933

- Female: 2700-2750 long; tail with short appendix; excretory pore not evident; oesophageal corpus linear; vulva about half way along corpus; one ovary; lateral crest of egg without bosses.....P. australasiae (Pessoa & Correa, 1926) Travassos, 1929

10.- Female: length of head to vulva > 270; eggs >100 long, without lateral groove.....11

- Female: length head to vulva < 230; eggs <85 long, with or without lateral groove.....12

11.- Female: 6000 long; 100 wide; cuticular annulations up to 20 wide; without ovijector; tail (188) acutely pointed; mouth opening triangular; excretory pore without lip; male: 610 long; spicule linear and acute.....P. aureus Cobb, 1920

- Female: 2980-4900 long, 130-310 wide; cuticular annulations 6-12 wide; with ovijector; tail (90-128) conical composed of diminishing conoids; mouth opening circular; excretory pore with lip; male: 840-1148; spicule round proximally, wide medially, pointed distally, linear but not acute.....*P. dalei*

12.- Female: 5500-7800 long; cuticular annulations anterior to vulva broad, salient; egg with lateral groove.....*P. galebi* Schwenck, 1926

Female: <5650 long; cuticular annulations anterior to vulva narrow, smooth; egg with or without lateral groove.....13

13.- Female: 2300 long; vulva 6.5% of body length from anterior end; nerve ring 5.6% of body length from anterior end; tail plainly conical, egg with 2 lateral grooves.....*P. phyllodromi* Basir, 1942

- Female: 3440-5650 long; vulva 3.2-5.5% of body length from anterior end; nerve ring 2.2-4.3% of body length from anterior end; tail subulate or composed of diminishing convex conoids; egg without lateral grooves.....14

14.- Female: 5029-5147 long; posterior uterus reflexed about one sixth of a body length from posterior end; tail subulate; excretory pore without

lip; egg oval.....P. ituana

(Kloss, 1966) Zervos, 1986

(Section III, D)

- Female 3440-5650 long; posterior uterus reflexed about one third of a body length from anterior end; tail not subulate, composed of diminishing convex conoids; excretory pore with lip; egg cresentrically ovoid.....P. behorefi

Van Waerebeke, 1969

Subfamily Thelastominae Travassos, 1920

GENUS Blatticola Schwenck, 1926, EMENDED DIAGNOSIS

Thelastomatidae; body of fairly uniform diameter but tapering anteriorly and posteriorly. Females: mouth opening circular or sub-triangular; surrounded by eight sub-median papillae or labiopapillae and pair of small lateral amphids. Oesophagus tripartite, consisting of anterior subcylindrical corpus followed by an isthmus (often short) and posterior valvular bulb. Nerve ring around corpus. Intestine wide anteriad, then parallel or subparallel sided to rectum or wide posteriad. Rectal glands between rectum and anus sometimes distinct. Excretory pore in anterior third of body. Vulva in posterior quarter of body. Reproductive system monodelphic and prodelphic. Uterus may lead to well developed muscular vagina which forms an ovijector. Eggs oval or ellipsoidal, colourless, surface often punctate. Tail short, conical. Males: much smaller than females. Oesophagus tripartite. Nerve ring around oesophageal corpus or isthmus. Intestine sub-parallel sided to cloaca. Excretory pore posterior to

base of oesophagus. Testis single, reflexed or outstretched. Tail conical, with or without constrictions, 3-4 pairs of tail papillae. Spicule single, without capitulum. No gubernaculum. Females, males and juveniles found in hind gut of cockroaches. Geographic distribution: The type species Oxyuris blattae Graeffe, 1860 = Blatticola blattae (Graeffe, 1860) Chitwood, 1932 is probably as widespread as its cosmopolitan host, Blattella germanica Linn. Other species of Blatticola occur in Andhra Pradesh, India; Karachi, Pakistan; Banks Peninsula and Tararua Ranges, New Zealand.

Blatticola barryi n. sp. (Fig. III, E, 18-22; Table 4).

Description

Females (Fig. III, E, 18-20). Cuticle annules only evident anterior to oesophageal isthmus; annules 3-4 wide. Lip region slightly offset. Amphidial apertures not seen. Buccal capsule small (width= 8-12), indistinctly sclerotised. Oesophagus tripartite, anterior corpus sub-parallel sided, expanded slightly posteriad; isthmus distinct, expanded anteriad; posterior bulb with sculptured plates. Nerve ring in region of posterior swelling of corpus or just anterior to it. Intestine broadest slightly behind oesophagus, decreasing in width in region of excretory pore, then sub-parallel sided to rectum. Rectal glands at junction of intestine and rectum distinct. Excretory pore near anterior extremity of ovary, not seen in all specimens. Vulva within 20% of a body length from posterior end, leading to very muscular vagina which forms an ovijector. Ovary originates in anterior third of body, passes posteriad for a short distance, reflexed to pass anteriad, then reflexed again in region of narrowing of intestine to pass posteriad beneath intestine. Ovary leads to a reflexed oviduct between

Figure III, E, 18–28

Blatticola barryi from *Celatoblatta quinquemaculata* and *Suifunema mackenziei* from *Celatoblatta undulivitta*.

18–20, *B. barryi*: 18–20, female: (18) entire; (19) head, lateral view; (20) tail. 21–22, male: (21) anterior end; (22) tail.

23–28, *S. mackenziei*: (23) female, anterior end; (24) female, vulva, vagina; (25) male, entire; (26) male, tail; (27) female, tail; (28) female, entire.

(Scale lines in μm.)

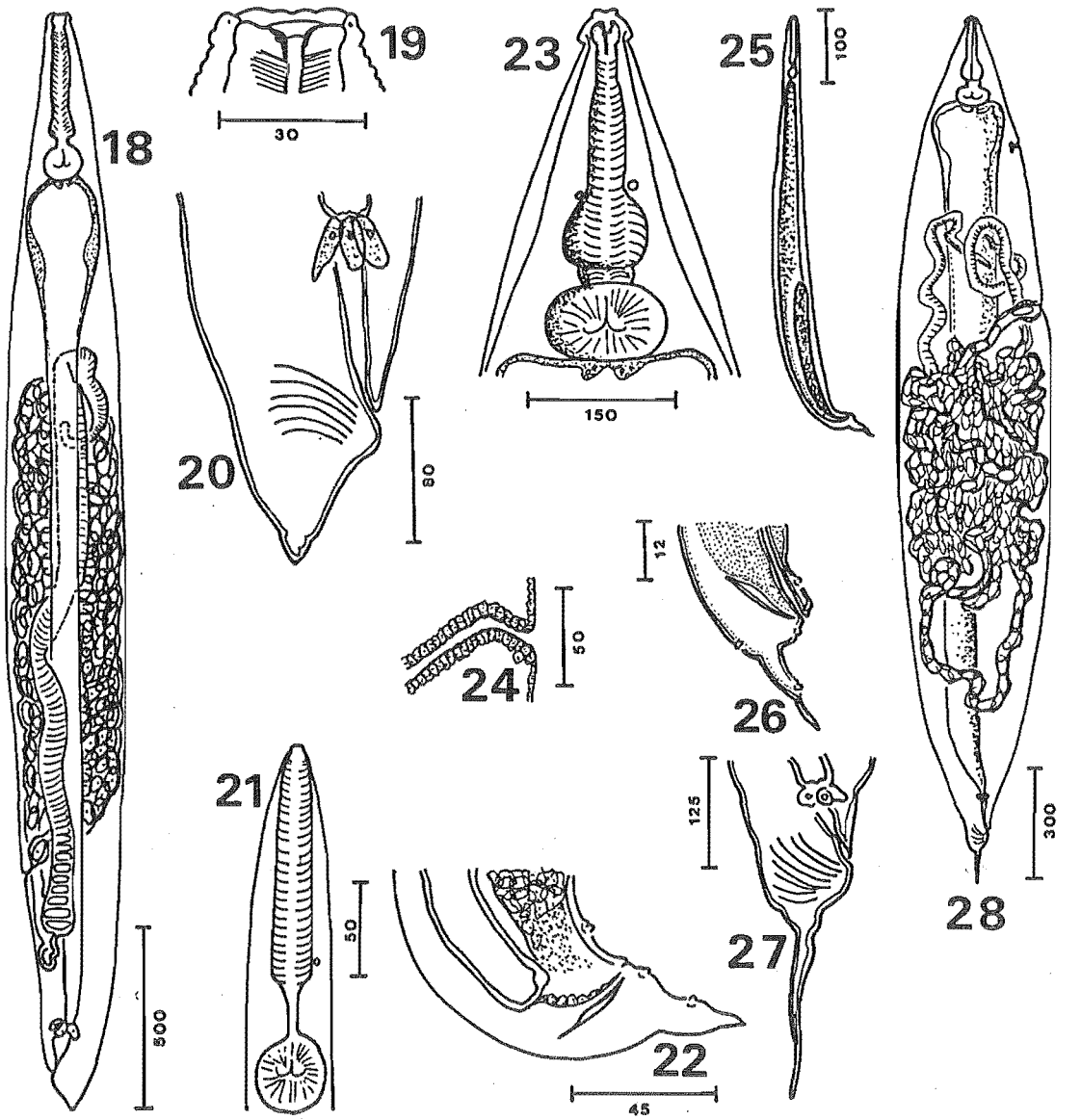
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Table 4. Dimensions (µm) of the type specimens of Blatticola barryi (ranges in parentheses, - = no measurement).

	Holotype female	Allotype male	Paratype females (n=11)	Paratype males (n=3)
Length	3180	1112	2995±10 (2430-3480)	1030,1080,1100
Width (maximum)	320	92	316±13 (230-360)	73,80,84
Width at bulb	168	56	167±17 (110-210)	52,60,70
Width at anus	72	24	78±2 (70-81)	30,30,30
Length of oesophagus	388	193	385±9 (360-450)	192,194,200
Length of corpus	272	124	267±7 (230-330)	124,124,130
Length of isthmus	32	36	35±2 (20-40)	30,32,36
Length of bulb	84	36	82±3 (70-100)	40,40,44
Width of bulb	88	-	94±3 (80-100)	-
Head to nerve ring	252	116	231±6 (200-260)	96,100,120
Head to excretory pore	84	-	77±5 (72-84)	-
Length intestinal/rectal gland junction to anus	144	-	120±6 (100-144)	-
Head to anterior extremity of anterior ovary	1000	-	1068±40 (940-1190)	-
Tail to posterior extremity of posterior ovary	-	-	428±26 (330-480)	-
Head to vulva	2572	-	2381±15 (1760-2920)	-
Tail to anus	72	44	78±2 (70-80)	40,48,60
Length tail to posterior-most papillae	-	28	-	20,30,40
Head to anterior extremity of testis	-	524	-	510,600,610
Length of spicule	-	20	-	20,20,20
Egg	175x66			

anus and vulva, oviduct leads to anteriorly directed uterus. Uterus single, reflexed in region of anterior flexure of ovary, passes posteriad to join vagina. Eggs asymetrically ovoid; slightly broader at one end, surface punctate, shell of uniform thickness throughout, operculum not seen. Tail very short, conical, formed of two indistinct convex conoids of diminishing size, cuticle of tail tip variously thickened to form pattern of internal body wall in optical section.

Male (Fig. III, E, 21-22). Cuticle indistincly annulated anterior to oesophageal isthmus, smooth posteriad. Lips slightly offset. Amphidial apertures and labial papillae, not seen. Oesophagus tripartite, corpus cylindrical, isthmus long, distinct from corpus but merging with bulb, bulb valve plates indistinctly sculptured. Nerve ring about 2/3 along corpus from anterior end. Intestine sub-parallel sided to cloaca. Excretory pore not seen. Testis extends anteriad, then reflexed posteriad at about mid body point to originate in posterior third of body. Spicule small, unornamented, linear, tapering to a point proximally and distally, broadest at middle, without capitulum. No gubernaculum. Tail tapering cone, with two shallow constrictions. Three pairs of ventro-lateral papillae; one pair pre-anal, two pairs post-anal.

Type data. Holotype female, allotype male and 15 paratypes (12 female, 3 male) in the New Zealand National Nematode Collection, Entomology Division, Department of Scientific and Industrial Reasearch, Auckland (holotype female, NZNNC holotype no. XXX; allotype male NZNNC XXX; 12 paratype females, NZNNC XXX-X; 3 paratype males NZNNC XXX-X).

Type host: Celatoblatta quinquemaculata Johns, 1966. Site in host: anterior end of colon of hind gut.

Type locality: Rock and Pillar Ranges, central Otago, South Island, New Zealand (45° 25' 0"S, 170° 5' 0"E); elevation 1000 m; 21/3/1981.

Remarks: The species is named for the New Zealand neurophysiologist Dr. Barry O'Brien, who collected the hosts.

TAXONOMY AND DIFFERENTIAL DIAGNOSIS

Some characteristics used in differential diagnosis are from redescriptions or dimensions given by authors (Ahmed & Jabin, 1966; Bozeman, 1942; Chitwood, 1930; Groschaft, 1956) other than those who initially described some species.

Females: B. barryi females have a suite of characters that distinguish them from other species of Blatticola (Appendix 3) that include: an intestine subparallel sided to rectum (as have others except B. opisthoplatia Ahmed & Jabin, 1966 and B. blattae, which have an expanded posterior intestine); distinct rectal glands (as have others except B. supellaimae Rao & Rao, 1956 and B. tuapakae); thickened, patterned tail cuticle (as has B. monandros, but not others); vulva more than 16% of body length from the anus (as has B. opisthoplatia but not others, in which the vulva is less than 13% of a body length from the anus); a doubly reflexed ovary (as have B. blattae and B. tuapakae but not others, which have a singly reflexed ovary); and a linear tail (as have others except B. tuapakae, which has a subulate tail, and B. opisthoplatia in which the tail is bluntly then sharply conical).

Males: B. barryi males have a suite of characters that distinguish them from other species of Blatticola (Appendix 3) that

include: cuticular annuli only obvious anteriad (as have others except B. opisthoplatia and B. supellaimae, which have annules over the entire body); a nerve ring near the posterior end of the oesophageal corpus (anterior or posterior to this in others); a cylindrical corpus (as have B. opisthoplatia and B. blattae but not others, which have a corpus of uneven width); a reflexed testis (as have others except B. opisthoplatia and B. blattae, which have an outstretched testis); 3 pairs of tail papillae (as have B. tuapakae and B. monandros, but not others, which have 4); and a tapering conoid tail with 2 constrictions (as have B. monandros, but not others). B. barryi males are the longest in the genus.

The confused taxonomic history of the genus Blatticola and of the type species B. blattae was clarified by Dale, 1966. The emended diagnosis of the genus given earlier was modified to accomodate B. barryi and species described since Chitwood's (1932) revision of the thelastomatids. As no key exists for species in this genus, one is given here.

KEY TO SPECIES IN THE GENUS Blatticola

1. - Female: intestine tapering posteriorly
male: reflexed testis; nerve ring around corpus.....2

- Female: posterior intestine broader than medial intestine;
male: outstretched testis; nerve ring around isthmus.....5

2. - Female: distance vulva to anus about 5% of body length;
ovary singly reflexed; male: 4 pairs tail
papillae; cuticle annulated throughout;
tail conical, with sharp linear point; nerve ring

around first half of corpus; corpus broadest medially.....*B. supellaimae* Rao & Rao, 1965

- Female: distance vulva to anus 7-17% of body length; ovary singly or doubly reflexed; male: 3 pairs tail papillae; cuticle annulated only anteriad; tail without sharply linear point; nerve ring around second half of corpus; corpus not broadest medially.....3

3. - Female: 1440-2740; ovary singly reflexed; egg with operculum; male: corpus flask-shaped; spicule <15.....*B. monandros* Zervos, 1983 (Section III, C)

- Female: 2430-4470; ovary doubly reflexed; egg with or without operculum; male: corpus cylindrical or broadest anteriad; spicule 17-22.....4

4. - Female: tail <3% of body length; distinct rectal glands; distance vulva to anus about 17% of body length; egg with operculum; male: tail tapering cone with 2 shallow constrictions; corpus cylindrical.....*B. barryi*

- Female: tail >7% of body length; rectal glands apparently absent; distance vulva to anus about 7% of body length; egg without operculum; male: tail convex conoid then elongate, tending subulate near tip; corpus broadest anteriad.....*B. tuapakae* Dale, 1966

5. - Female: nerve ring about two thirds along corpus from anterior end; ovary not doubly reflexed; tail about 4% of body length; egg 259x75; male: spicule 34-50; tail about 35.....B. opisthoplatia Ahmed & Jabin, 1966

- Female: tail about 8% of body length; nerve ring near base of corpus; ovary doubly reflexed; egg 120x40; male: spicule about 20; tail about 62-80.....B. blattae (Graeffe, 1860) Chitwood, 1932

Subfamily Thelastominae Travassos, 1920

GENUS Suifunema CHITWOOD, 1932, EMENDED DIAGNOSIS

Thelastomatidae; body of fairly uniform diameter but tapering anteriorly and posteriorly. Females: mouth opening prismoidal, lips offset, eight submedian labiopapillae; amphids present. Oesophagus tripartite, consisting of a simple cylindrical or posteriorly swollen distinct anterior corpus, an isthmus set off from corpus and distinctly or not distinctly set off from posterior valvular bulb. Nerve ring encircles corpus or isthmus. Intestine sub-parallel sided to anus. Rectal glands sometimes distinct at junction of intestine and rectum. Excretory pore between base of oesophagus and anterior extremity of ovary. Vulva anteriad, approximately 25-40 per cent of body length from anterior end, leading to muscular ovijector. Reproductive system didelphic, both ovaries in anterior part of body. Eggs oval, or ovoid with one side flattened, with operculum. Tail short, bluntly rounded or slightly conical, bearing a filiform projection. Males: much smaller

than females. Body broadest about three quarters of a body length from anterior end. Oesophagus indistinct. Testis single, outstretched. Tail round, with short caudal projection, four pairs of tail papillae (three pairs ventro-lateral, one pair dorso-lateral). Single spicule. Males, females and juveniles in the anterior hind gut (colon) of cockroaches. Geographic distribution: China, Turkey, New Zealand.

Type species: Suifunema caudelli Chitwood, 1932

Suifunema mackenziei n. sp. (Fig. III, E, 23-30, Table 5).

Description

Female (Fig. III, E, 23-24, 27-30). Cuticle annulated, first annule 20 wide, subsequent annules about 4 wide; annules flatten out and become indistinguishable in posterior quarter of body. Lip region offset (Fig. 23); amphids small. Buccal capsule small (width 7-8), distinctly sclerotised. Oesophagus tripartite, corpus expanded posteriorly into a pseudobulb almost the width of the bulb (Fig. 29); isthmus distinct from corpus and bulb, expanded slightly at anterior end or in the middle; bulb broader than long, plates distinctly sculptured (Fig. 29). Nerve ring about half way along corpus. Intestine broadest behind oesophagus, then sub-parallel sided to rectum. Rectal glands distinct between intestine and rectum. Excretory pore between base of oesophagus and anterior extremity of uterus. Vulva about one third of a body length from anterior end. Vagina muscular, forming an ovijector. Reproductive system didelphic. Ovaries originate in anterior third of body; in some females, one ovary originates posteriad, passes anteriad, then reflexed posteriad; the other originates anteriad, passes posteriad, is reflexed anteriad, then reflexed again to pass posteriad; in other (possibly older) females, both ovaries much coiled and reflexed just posterior to oesophagus. Ovaries both pass to much coiled uteri packed

Table 5. Dimensions (μm) of the type specimens of Suifunema mackenziei (ranges in parentheses, - = no measurement).

	Holotype female	Allotype male	Paratype females (n=6)	Paratype males (n=2)
Length	3772	604	2720±17 (2200-3772)	520,560
Width (maximum)	468	44	378±5 (260-560)	36,44
Width at bulb	248	20	208±15 (160-250)	20,24
Width at anus	108	16	85±7 (72-108)	12,20
Length of oesophagus	376	80	335±8 (320-376)	68,84
Length of corpus	264	-	232±7 (220-270)	-
Length of isthmus	28	-	20±2 (20-30)	-
Length of bulb	84	-	80±4 (70-90)	14,16
Width of bulb	120	-	105±3 (100-120)	-
Head to nerve ring	140	-	-	-
Head to excretory pore	580	-	460±34 (400-580)	-
Length intestinal/rectal gland junction to anus	140	-	-	-
Head to anterior extremity of anterior ovary	656	-	513±34 (400-640)	-
Head to vulva	1240	-	865±13 (780-1240)	-
Tail to anus	288	24	268±8 (250-290)	28,28
Length tail to posterior-most papillae	-	16	-	16,18
Head to anterior extremity of testis	-	320	-	360,368
Length of spicule	-	18	-	18
Egg	80x28			

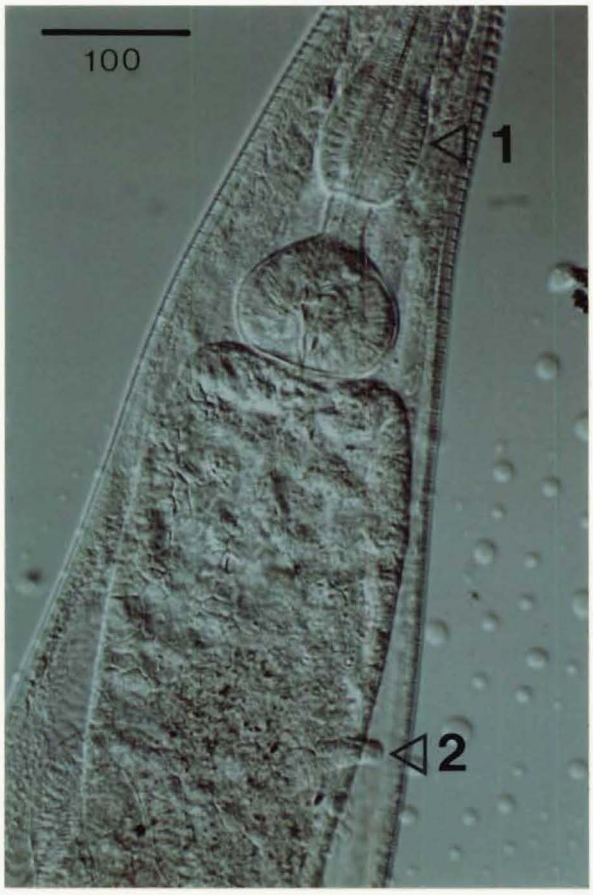
Figure III, E, 29-30

Suifunema mackenziei from Celatoblatta undulivitta.

29, anterior end of female showing posterior expansion of oesophageal corpus (arrow 1), distinct isthmus, broad bulb, and ovary (arrow 2).

30, active form juvenile released through operculum of egg by pressure on cover slip. Note punctate surface of egg.

(Scale lines in μm.)



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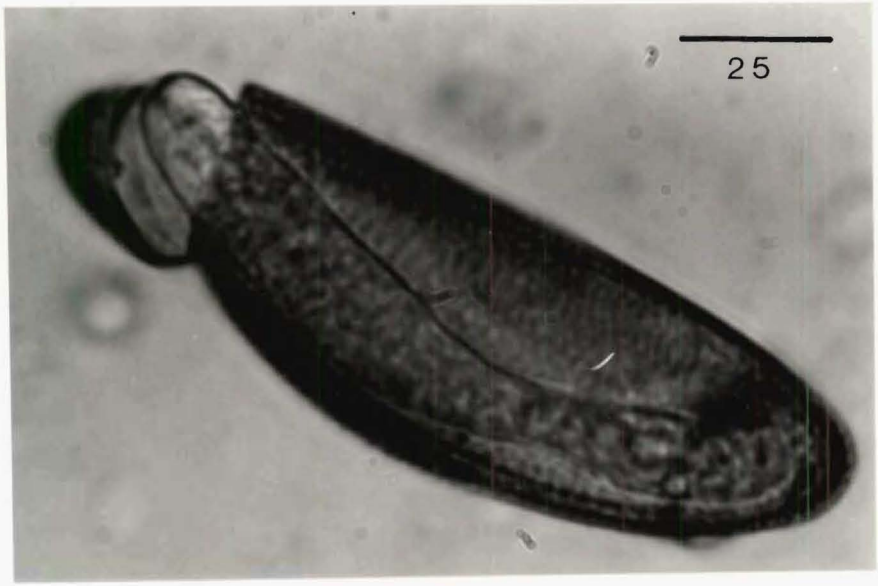


30

with numerous eggs; uteri unite to form a common uterus which leads to the ovijector. Eggs (Fig. 30) oval, flattened on one side, slightly broader at one end, surface punctate, with operculum. Tail (Fig. 27) very short, bluntly rounded, with a short, filiform projection.

Male (Fig. III, E, 25-26). Much smaller than female. Cuticle minutely annulated, annules more obvious posteriad. Lips minute, offset. Amphidial apertures and labial papillae not seen. Oesophageal regions indistinct. Nerve ring and excretory pore, not seen. Intestine parallel sided. Testis single, outstretched. Spicule very small, parallel sided except tapering to a point proximally and distally, without capitulum. No gubernaculum. Tail (Fig. 26) round, with short, filiform projection. Four pairs of tail papillae; three pairs ventro-lateral (one pair pre-anal, two pairs post-anal), one pair dorso-lateral.

Type data. Holotype female, allotype male and 9 paratypes (5 female, 4 male) in New Zealand National Nematode Collection, Entomology Division, Department of Scientific and Industrial Research, Auckland (holotype female, NZNNC holotype no. XXX; allotype male, NZNNC XXX; paratype females, NZNNC XXX-X; paratype males NZNNC XXX-X).

Type host: Celatoblatta undulivitta (Walker, 1868), Johns, 1966. Site in host: anterior end of colon of hind gut.

Type locality: Lower Hutt, North Island, New Zealand (41° 12' 0" S, 174° 58' 0" E); elevation 100 m; 27/5/1982.

Remarks: The species is named for the New Zealand nematologist, Ms. Jan McKenzie.

TAXONOMY AND DIFFERENTIAL DIAGNOSIS

Only one species has been described in the genus Suifunema so far. S. caudelli Chitwood, 1932 occurs in the cockroach Stelopyga sinensis Walker in China (Chitwood, 1932) and Turkey (Mimioglu & Sahin, 1976). This is the first record of a Suifunema in a New Zealand host. S. mackenziei females possess a suite of characters that distinguish them from S. caudelli females. These include: dimensions larger overall; a corpus pseudobulb (no pseudobulb in S. caudelli); a nerve ring around the corpus (not isthmus as in S. caudelli); longer, narrower eggs which lack a conspicuous opercular cap (cap in S. caudelli); a longer tail with longer filiform projection; and prominent rectal glands (not described in S. caudelli). Comparison of males can not be made because S. caudelli males are unknown. The emended diagnosis of the genus given earlier was modified to accomodate the new species and include a description of the male.

GENERAL REMARKS

All nematodes described here were found in the anterior part of the colon of the hind gut. The much smaller male lay anterior to the female or near her anterior end. The majority of females lay outstretched with the head directed anteriorly; in only a few cases were females reflexed so that the tail was also directed anteriorly. In all but one case, there was no visible evidence of damage to the host. Thus these thelastomatids are probably benign, as are other thelastomatids (Poinar, 1975).

PARASITE DISTRIBUTIONS

Protrellus dalei, like its type host Celatoblatta vulgaris, is widespread. This nematode is also found in C. peninsularis, which

is restricted to Banks Peninsula, Canterbury, and C. brunni, which is restricted to the Chatham Island Group. C. vulgaris is unknown on Banks Peninsula or the Chatham Islands (Johns, 1966), but as the three cockroach species host the same parasite species, it is likely that they were once sympatric. C. vulgaris, C. brunni and C. peninsularis are certainly very closely related species (P. M. Johns, Department of Zoology, University of Canterbury, New Zealand, pers. comm.). The only other cockroach on Banks Peninsula is Parellipsidion pachycercum, which, although sympatric with C. peninsularis, never contains P. dalei. Instead, it contains a thelastomatid (Blatticola monandros) which is apparently specific to it (Section III, C). C. brunni is the only cockroach species on the Chatham Islands. Comment cannot be made on the relationships of the other nematodes described in this paper because of lack of data, but further work may show taxonomic and/or ecological relationships within the host-parasite groups.

F) Blatticola blattae (GRAEFFE, 1860) CHITWOOD, 1932

Blatticola blattae has been recorded from Blatta orientalis, B. aegyptiaca, Ectobia laponica and E. livida as well as from Blattella germanica. It can be distinguished from all other species in the genus by the shape of the female intestine, and by the outstretched testis and position of the nerve cord in the male (Section III, E). It is one of the most extensively studied thelastomatids (for example, see Bozeman, 1942; Cali & Mai, 1965) and much is known about its life history and ultrastructure. Females are oviparous, laying eggs which pass out in the host faeces. In the external environment, development and moulting of the juvenile within the egg proceed until a resting infective stage is reached. Only juveniles that have reached this stage are infective to the next host.

G) EGG DEVELOPMENT IN Protrellus dixoni

Eggs from female P. dixoni removed from Drymaplaneta variegata are oval with one end rounded, the other slightly pointed (Section III, D). Embryos within eggs at room temperature took about 48 hours to reach a vermiform stage in which the developing gut was discernible. By 72 hours, juveniles were active, and the divisions of the gut, including the bulb with its sculptured plates, were obvious. Juveniles were longer than their shell and the posterior end was reflexed so that the developing nematode could be accommodated. A similar stage is seen in Protrellus dalei (Fig. III, E, 13). Activity consisted of twisting the whole body, but the anterior end of the juvenile always remained at the rounded end of the egg. Juveniles appeared to probe the inner lining of the shell with their lips, which they extened and

retracted while moving their anterior end back and forth. By 90-110 hours, movement had ceased and juveniles had shrunk to about 2/3 of the length of the shell (Fig. III, D, 14). This stage resembled the resting infective stage of Blatticola blattae (Section III, F), and a similar stage occurs in P. dalei (Fig. III, E, 15). Such juveniles were infective to cockroaches. By 240 hours, juveniles had shrunk to about half the length of the shell. The divisions of the gut were still discernible, but the intestine was folded upon itself several times. Eggs remained in this state and were viable for up to 120 days after removal from female nematodes (Section IV, F) and possibly longer. At no stage during development in the eggs was the sex of juveniles able to be determined.

H) ARE THELASTOMATIDS PARASITES?

Arguments concerning the nature of parasitism are many and varied. Leuckart (1879, cited by Dogiel, 1962) defined parasites as "creatures which find their nourishment and habitat on other living organisms", and suggested that parasitism is a type of predation determined mainly by the comparative small size of the predator compared to the prey. Some later authors considered that the single criterion of the mode of feeding is insufficient to define parasitism, and attempted to clarify the concept by adding another distinguishing feature, the harmful effect of the parasite on the host. On the criterion of damage, thelastomatids would be excluded as parasites because they are apparently harmless.

The concept of harm to the host as a necessary feature of parasitism is inadmissible for several reasons. Firstly, parasites exhibit a wide range of variability in the degree of harm or damage they

cause to their host. At one extreme, parasites merge into the parasitoid type of association, killing their host and thus resembling predators. At the other extreme are the symbionts which live on or in the host with a degree of nutritional dependence that may be one sided and/or facultative (eg., commensalism) or mutual and obligatory (eg., mutualism), but in which damage to the host is not apparent. Secondly, a given relationship may be beneficial to the host in one environmental context and damaging in another. Thirdly, on the criterion of damage, all predators would become parasites, especially those that maimed their potential prey. Finally, as Filipchenko (1937, cited by Dogiel, 1962) observed, it is not permissible to characterise an entity (the parasite) by the attribute (damage) belonging exclusively to another entity (the host).

Dogiel (1962) defined parasites as "those animals which use other living animals as their environment and source of food, at the same time relinquishing to their host, partly or completely, the task of regulating their relationship with their environment". Thus Dogiel avoided the question of damage to the host. For the puposes of discussion in this thesis, Dogiel's definition is adopted. Thus thelastomatids are parasites because they use other living organisms as their environment, and this association appears to be obligatory. No free living thelastomatids have been found and none cultured on artificial media. It has not been determined if their nourishment consists of partially digested food, or microbes in the host gut, or both, but most, as far as is known, are specific to their particular host or group of hosts. This implies that their needs are also specific, and that these needs must be supplied by a host and are not found in the external environment.

SECTION IV

PARASITE POPULATION BIOLOGY

SECTION IV

PARASITE POPULATION BIOLOGY

A) INTRODUCTION

Evidence for population regulation of thelastomatids studied is presented from field (Section IV, B, E) and laboratory work (Section IV, F). In most instances, regulation is mediated by a density-dependent mechanism, but the effects of density-independent climatic factors are also considered (Section IV, D). Discussion of the possible mechanisms responsible for the observed distribution patterns is presented in Section IV, F.

The effect of crowding on egg production and the cyclical production of eggs in batches is discussed (Section IV, C, F). Evidence for parthenogenetic arrhenotoky in Protrellus dixoni is presented (Section IV, F).

B) EVIDENCE FOR POPULATION REGULATION OF A MONOGAMOUS THELASTOMATID NEMATODE IN COCKROACHES

Abstract

Blatticola monandros Zervos lives in the the hind gut of the endemic New Zealand cockroach Parellipsidion pachycercum Johns. Infection incidence was high (54%) in small nymphs and increased further with cockroach size to a maximum (92%) in penultimate nymphs. Mean and maximum intensity of nematodes decreased with increasing host size. The modal infrapopulation type consisted of one adult male and one adult female. Other infrapopulations were transitional to this type. Monogamous infrapopulations increased in prevalence with increased host size. Juvenile males were uncommon and probably develop faster into adults than juvenile females. Infrapopulations with two juvenile males were very rare and no cockroach contained two adult males. Regulation of infrapopulation size and structure occurs through a density-dependent and sex-dependent reduction in infection intensity leading, unusually, to an under-dispersed distribution pattern. Possible regulatory mechanisms are discussed.

INTRODUCTION

Few data are available concerning population structure and regulation of insect parasitic nematodes from field collected hosts, and almost none concerning thelastomatids. Knowledge of thelastomatids usually consists of single collection records, although life histories are known from a few laboratory reared hosts. Blatticola monandros Zervos, 1983 (Oxyuroidea: Thelastomatidae; Section III, C) occurs in the hind gut of the endemic New Zealand cockroach Parellipsidion

pachycercum Johns, 1966 (Blattellidae) and in this paper, evidence is presented showing that regulation of the parasite population occurs, and that this regulation leads to monogamy in most established infrapopulations.

METHODS

Nymphs and adults of P.pachycercum (n=4135) were collected from amongst the foliaceous bark on the trunks of fuchsia trees (Fuchsia excorticata (J.R. et G. Forst) Linn.f), in a patch of forest at Kaituna Valley, Banks Peninsula, Canterbury, New Zealand (43°43'15"S., 172°45'30"E.; elevation 250 m) between March 1981 and February 1984. Cockroaches were killed by crushing the nerve cord behind the head, viewed with a stereomicroscope and dissected in cockroach saline. Cockroaches were assigned to 6 sub-adult size classes (each probably represents an instar) and one adult class based on interocular distance and hind femur length (Zervos, 1984; Section II, B).

The number, position in the hind gut, developmental stage, and sex of nematodes in each infrapopulation were noted. B. monandros females were assigned to one of 3 juvenile stages on the basis of total length, but immature males could not be so assigned because their measurements overlapped too much (Zervos, 1983; Section III, C). Immature males were recognisable by their having a fully developed spicule, but no gonads. Cockroach oothecae and their developing nymphs, cast exuviae, newly-moulted cockroaches, and host faecal pellets were examined for nematodes and their eggs. To overcome difficulties arising from defining parasite populations in the same terms as free-living populations, terminology proposed by Margolis, Esch, Holmes, Kuris & Schad (1982) is used. Thus the suprapopulation consists of all individuals of a given parasite species in all stages of development

within all hosts in a particular ecosystem whereas those in an individual host constitute an infrapopulation. Prevalence defines the percentage of infected hosts and intensity is the number of a particular parasite species in each infrapopulation.

RESULTS

i) Location of nematodes

B. monandros was always found in the anterior part of the hind gut. When only juveniles were present they appeared to be randomly distributed in this region, but when adults were present the male was in the "green cap region" (Zervos, 1984; Section II, B) just anterior to the female (Fig. IV, B, 1). Single females usually lay with the body reflexed so that the head and tail lay anteriorly. If more than one adult female was present, the heads of all were directed anteriorly but the bodies of all but one were outstretched and extended into the posterior part of the hind gut. Only one lay with the body reflexed.

Many newly-moulted cockroaches in each size class were found to harbour still active juvenile or adult nematodes, but no nematodes were found on freshly cast exuviae. Developing cockroach nymphs in oothecae and oothecae themselves did not contain nematodes or their eggs. Eggs were found only on host faecal pellets. Tissue damage of the hind gut was observed in only 1 of 3393 infected P. pachycercum and no infected host was observed to exhibit obviously abnormal behavioural traits.

ii) Size class infection prevalence

Infection prevalence was high in the smallest (class 1) cockroaches, increased in larger (older) nymphs, then declined in sub adults and adults (Fig.IV, B, 1). No significant difference in infection prevalence was found between adult male and female hosts (Anova, $F < 1$, n.s.).

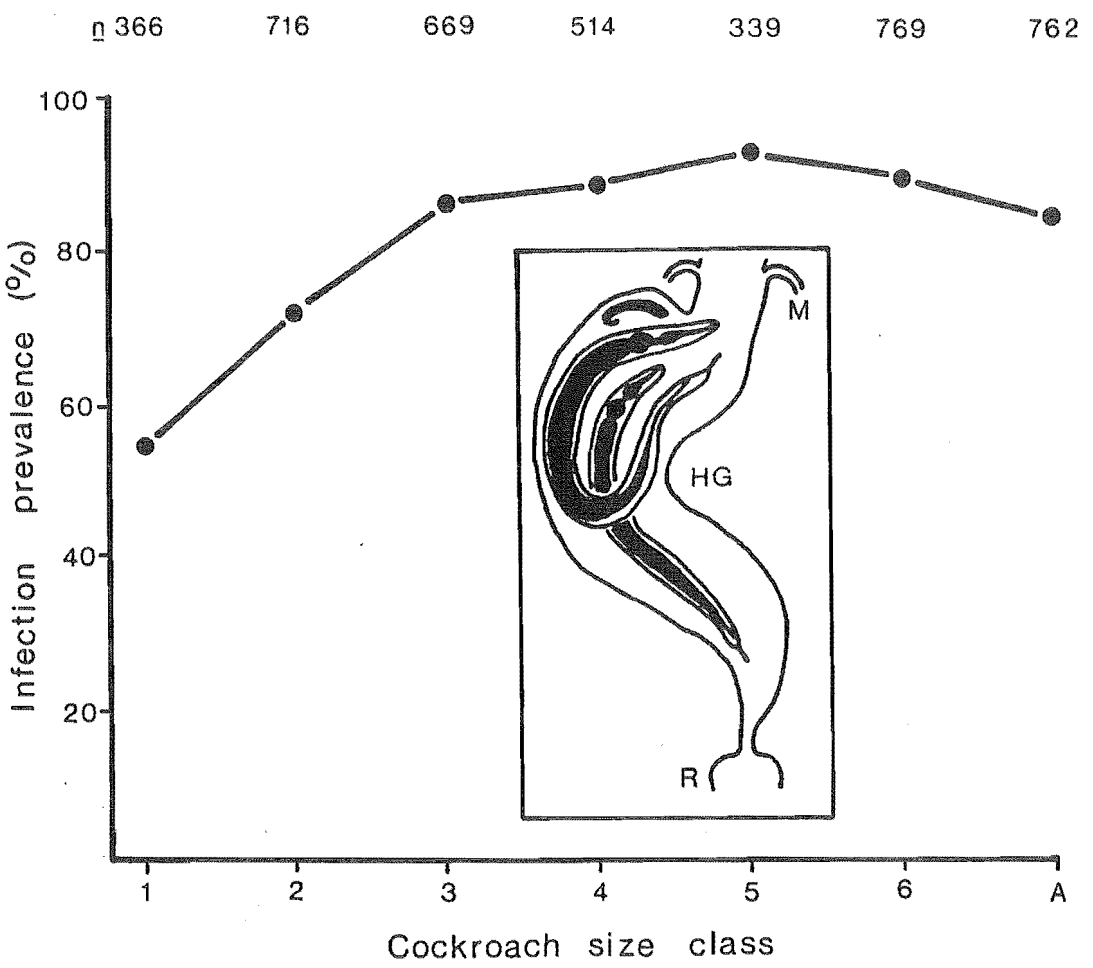


Figure IV, B, 1

Percentage of Parellipsidion pachycercum in each size class infected with Blatticola monandros

Cockroach size class 1-6, nymphs; A, adults. Total cockroaches per class (n) above graph.

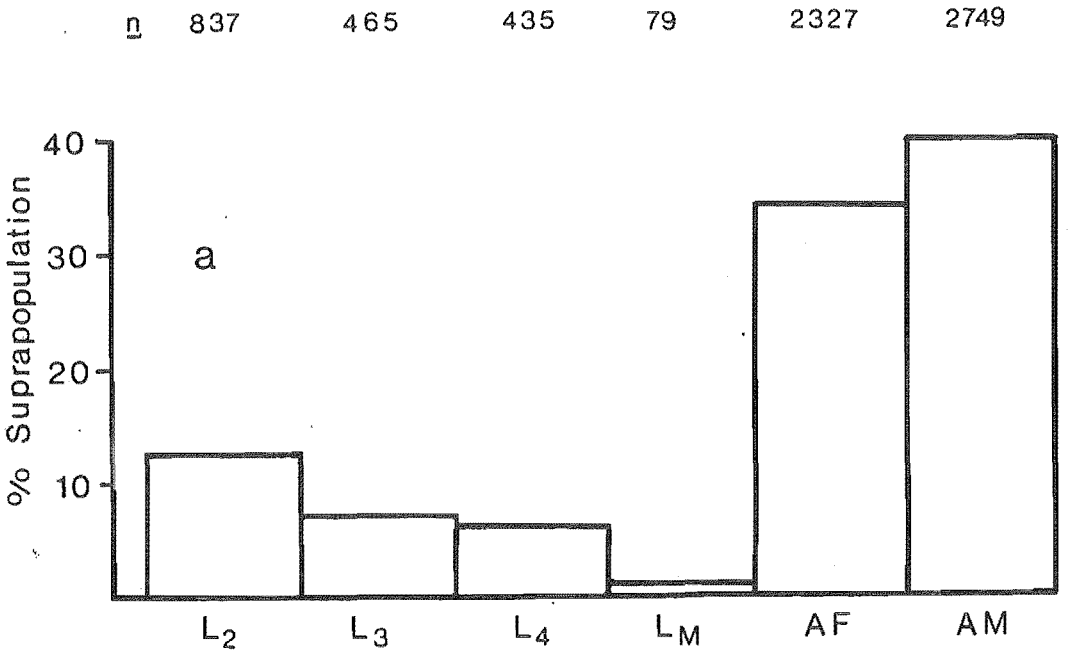
Inset, position of male (small) and female (large) nematodes in the hindgut (HG). M, malphigian tubules; R, rectum.

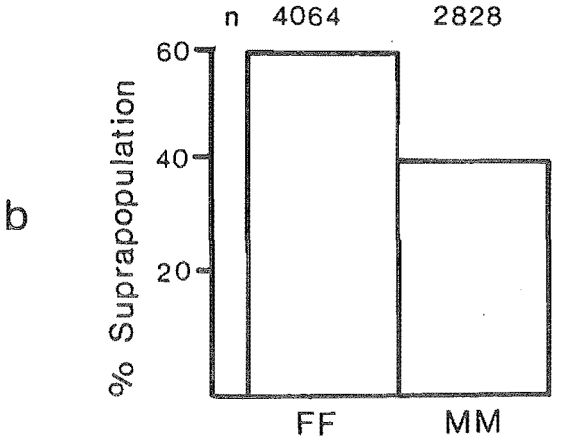
Figure IV, B, 2

Percentage distribution of Blatticola monandros in the suprapopulation.

(a), by developmental stage. L_2-L_4, juvenile females; L_M, juvenile males; AF, adult females; AM, adult males.

(b), by sex, regardless of developmental stage. FF, all females; MM all males. Total n of each type, above graph.


n 837 465 435 79 2327 2749
40
30
20
10
% Suprapopulation
a
L2 L3 L4 LM AF AM


n 4064 2828
60
40
20
% Suprapopulation
b
FF MM

iii) Nematode suprapopulation structure

Adults predominated in the suprapopulation but there were fewer adult females than adult males. However, when all stages were considered, females predominated over males (Fig. IV, B, 2).

iv) Nematode infrapopulation structure

The predominant infrapopulation type (monogamous infrapopulations, Fig. IV, B, 3) comprised 1 adult male and 1 adult female. Other common infrapopulation structures observed were an adult male with or without a juvenile female(s) and juvenile female(s) alone. Eighty-one percent of all infected hosts had 1 adult male with or without juvenile and/or adult female(s). No infrapopulation included more than one adult male although a few had 2 or, rarely, 3 or 4 adult females (with or without males). In adult hosts, adult female B. monandros in infrapopulations containing 2 or more adult females were smaller (mean length, 1.74mm, n = 47) than single adult females (mean length, 2.18mm, n=60 ; Anova, $P < 10^{-4}$). In such infrapopulations, the anteriormost adult female was the larger. Only 0.15% of all infrapopulations had 2 juvenile males,and they were always accompanied by one or more females.

Prevalence of monogamy was lowest in smallest cockroach nymphs but increased in larger hosts whereas the number of cockroaches with juvenile females (with or without a male) decreased (Fig. IV, B, 4). No class 1 host supported adult females without a male, although some lone adult males occurred in this class. The increase in miscellaneous infrapopulations in older cockroaches was mainly due to an increase in infrapopulations having an adult female(s) only, although some of these miscellaneous infrapopulations (eg., in 9.3% of adult hosts) comprised an adult male with 2 or, rarely, more adult females.

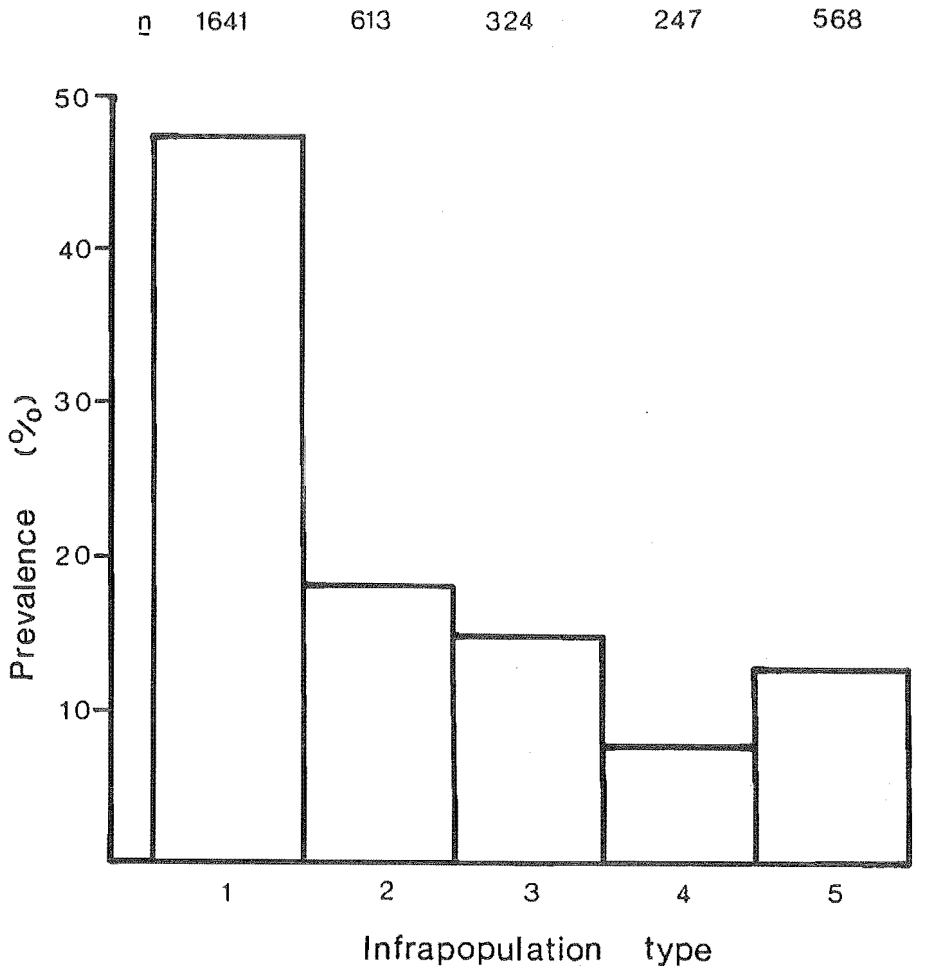


Figure IV, B, 3

Prevalence of Blatticola monandros infrapopulation types (regardless of host size class).

1, 1 adult male and 1 adult female (monogamous infrapopulations); 2, 1 adult male and juvenile female(s); 3, juvenile female(s) only; 4, 1 adult male; 5, miscellaneous infrapopulations (1 adult male and 2^{+} adult females, n= 138; 1 adult male and adult female(s) and juvenile female(s), n= 110; adult female(s) only, n= 210; adult female(s) and juvenile female(s), n= 36; juvenile male(s) with or without female(s). n= 74). Total n of each infrapopulation type above graph.

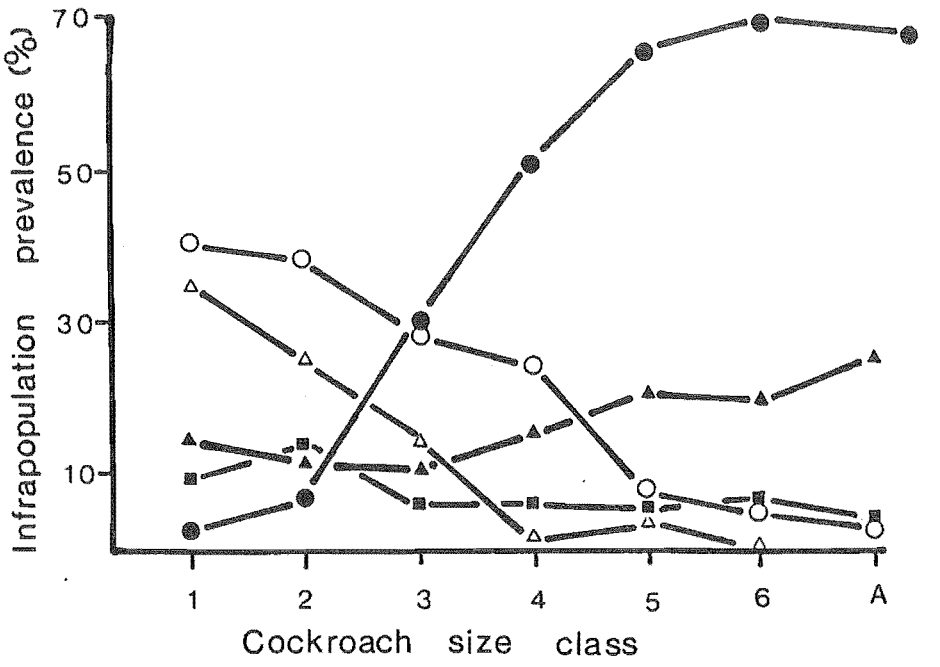


Figure IV, B, 4

Prevalence of Blatticola monandros infrapopulation types in each size class of Parellipsidion pachycercum (% of infected hosts only).

Solid circles, monogamous infrapopulations; open circles, 1 adult male and juvenile female(s); squares, 1 adult male; open triangles, juvenile female(s) only; solid triangle, miscellaneous infrapopulations (as for Fig. IV, B, 3).

v) Infection intensity

A selective reduction in infection intensity with an increase in host age was observed. In class 1, mean intensity was 2.5 worms/host, whereas in adult hosts it was 1.94. Class 1 and 2 P. pachycercum sometimes supported up to 7 small juvenile female B. monandros (with or without a male) while class 3 cockroaches usually supported only 1 or 2 larger sub-adult or adult female nematodes (with or without a male). In larger cockroaches a monogamous pair was the predominant group.

DISCUSSION

It seems likely that fuchsia bark is a major daylight habitat of Parellipsidion pachycercum as few were found in other habitats. Celatoblatta peninsularis Johns, 1966 (Blattidae), other non-blattid insects (in 9 Orders), and a variety of other invertebrates (in 4 Phyla) occur sympatrically with P. pachycercum. None of several hundred examined was infected with Blatticola monandros. As with other thelastomatids (Dobrovolny & Ackert, 1934; Poinar, 1975; Welch, 1963, 1965) B. monandros has a direct life cycle. These population data are, therefore, assumed to reflect the entire population of this nematode.

The results indicate that the size and structure of B. monandros infrapopulations are regulated through a density-dependent and sex-dependent reduction of intensity with host age. The main evidence for this is that monogamy predominates (Fig. IV, B, 3) and it can be inferred from host age data (Fig. IV, B, 4) that most other infra-population types are transitional only. For example, the number of infrapopulations consisting of juvenile females (with a male) decreased with host age as supernumerary females were lost, leaving only one to survive to adulthood. Similarly, the number of juvenile-female(s)-only

infrapopulations decreased with host age as a male was recruited to each and one female matured.

There are several possible explanations for the distribution patterns observed for these nematodes. These include a sex ratio of progeny skewed towards females; density-dependent environmental sex determination; differential mortality of overburdened hosts; control by the immune response of the host; direct physical interference competition between worms; indirect competition for space, food, or some other limiting factor; and/or indirect self-regulation by the production of some anthelmintic by the nematodes themselves.

The sex ratio of progeny and the effect of environment on sex determination is unknown for B. monandros. In some other entomogenous nematodes, environment affects sex determination, but the effect is expressed in a variety of ways and is dependent on genetic mechanisms which differ among those nematodes concerned (Caullery & Comas, 1928; Christie, 1929; Ezenwa & Carter, 1975; Parenti, 1965; Petersen, 1972).

As with other thelastomatids (Poinar, 1975), B. monandros is probably benign, because infected cockroaches were apparently not adversely affected. The distribution pattern of this nematode cannot, therefore, be attributed to differential parasite-induced mortality of over-burdened hosts. Nor can the pattern be attributed to host defensive responses. In arthropods, such responses are mediated almost exclusively by phagocytic haemocytes in the haemocoel (Wakelin, 1976). Control of gut parasites by immune responses in invertebrate hosts is unknown (Lackie, 1980) and probably does not exist. Physical interference competition was never seen amongst these nematodes when they were observed in various combinations in saline, and is unlikely because

B. monandros does not have structures such as spears that could be used in such competition.

Preferred positions in the hind gut and the smaller size of adult females when more than 1 were present per host suggest that competition for space or some other resource is a major limiting factor for this nematode. An additional adult female can survive at presumably less favoured gut sites though few do. Larger cockroaches are able to support an increased parasite biomass because both adult nematodes in a monogamous infrapopulation increase in size with increased host size (Zervos, 1983; Section III, C). This ability is not expressed as increased nematode intensity in larger hosts. If resource competition were solely the case, infrapopulations consisting of only 2 or 3 adult males should occur, as males are only one-third as large as females. No such infrapopulations were found.

Finally, infrapopulation size and structure may be regulated by the production of some anthelmintic by the nematodes themselves. Experimental evidence (Section IV, F) suggests that this is the case in another cockroach-thelastomatid system.

The effect of regulation on reduction of numbers of *B. monandros* in an infrapopulation is apparently not equal in initial intensity or speed between the sexes. Scarcity of juvenile males and of infrapopulations with 2 juvenile males suggest males develop more rapidly than females and that there is rigorous elimination of males at an early stage, whereas supernumerary females are eliminated more slowly. The presence of adult males (with or without female(s)) and the absence of lone adult females in class 1 nymphs also suggests that males develop more rapidly than females. In both sexes, adults probably live longer than juveniles. This can be inferred from the data because adults

predominate in the suprapopulation.

Lower prevalence of B. monandros in sub-adult and adult hosts (Fig. IV, B, 1) was not caused by poor initial recruitment because prevalence and intensity were generally high in small nymphs and could therefore be expected to remain so in larger cockroaches as these nematodes survive host moults. Instead, lower prevalence in older hosts may have been a result of senescence of B. monandros and poor replacement. It is possible that older cockroaches are not coprophagous and therefore avoid reinfection. Dobrovolny & Ackert (1934) also found prevalence of infection with the thelastomatid Leidynema appendiculata (Leidy, 1850) (Chitwood, 1932) to be higher in nymphs of the cockroach Periplaneta americana L. (instars not given); they suggested that an unspecified age-dependent resistance to nematode infection in adult hosts reduced prevalence.

Some other cockroach thelastomatids infrapopulations may be regulated in a manner similar to that observed in B. monandros. Hominick & Davey (1972a) never found more than one adult male Leidynema appendiculata in Periplaneta americana. Unfortunately, these authors gave few details of infrapopulations containing males but did suggest that the presence of 1 adult male inhibited development of other males and that environment controls sex differentiation in this species. Bozeman (1942) found 0-2 adult male and 0-4 adult female Blatticola blattae (Graeffe,1860) Chitwood,1932 in unsexed and female Blattella germanica L. and 0-1 adult male and 0-2 adult females in nymphs and males. However, distribution frequencies were not given. Chitwood (1930) noted infrapopulation structure for the same nematode in the same host. In most of these cockroaches, only a single adult female B. blattae was found with 1 or 2 males. Lee (1974) and Peregrine

(1974) found low numbers of male compared to female Thelastoma attenuatum in Periplaneta americana. Other investigations into thelastomatid infrapopulation structure have dealt with female nematodes only (Hominick & Davey, 1972b, 1973), but there is cryptic evidence in the literature which suggests that at least some are monogamous. For example, a number of thelastomatid descriptions have been based on nematodes from one cockroach host only (Basir, 1941, 1942; Farooqui, 1970 (some descriptions only); Rao & Rao, 1965 b,c, amongst others). Most such descriptions are based on only 1 adult male and 1 adult female. Monogamous infrapopulations are also the predominant infrapopulation type in several thelastomatids in other endemic New Zealand cockroach species (Section IV, E), and amongst undescribed thelastomatids in three endemic Australian cockroach species, only one male but several females may be found (Zervos, unpublished data).

Infrapopulation regulation may also occur amongst thelastomatids in arthropods other than cockroaches. Infrapopulations of Wetanema hula Dale, 1967 in the stenopelmatid Hemideina thoracica (White, 1846) are comprised predominantly of females (Zervos, unpublished data). With Thelastoma moko Bowie, 1983, never more than one adult male is found in its millipede host, Eumastigonus sp. (Bowie, 1983). Upton, Crawford & Hoffman (1983) found an average adult female to adult male ratio of 10:1 for Thelastoma collare Upton, Crawford & Hoffman, 1983 in the millipede Orthoporus ornatus (Girard, 1853), Causey, 1954. Amongst several thelastomatid species of crickets, Farooqui (1970) found only a single male but several females per host.

Amongst dioecious parasites other than thelastomatids, there are several comparison that can be made with the phenomenon of monogamy in B. monandros. Two species of Chitwoodchabaudia (Nematoda:

Chitwoodchabaudiidae), each specific to undescribed aquatic toads (Xenopus spp.) almost invariably have monogamous infrapopulations (R. C. Tinsley, School of Biological Sciences, Queen Mary College, University of London, England, pers. comm.). Amongst dioecious cestodes, Jarecka (1960) found that not more than 2 Diploposthe reach maturity in the duck Aythya nyroca (Guldenstadt) and that with D. sui-generis Kowalski, 1903, these were a male and a female. Self & Pipkin (1966) found 79% of dowitchers (Limnodromus scolopaceus (Say)) to be infected with a monogamous pair of Shipleya inermis Fuhramm, 1908, while Coil (1963) found all mature Charadrius wilsoni Ord infected with 1 male and 1 female Gyrocoelia pagollae Cable & Meyers, 1956.

Mechanisms that regulate parasite populations have received much attention in recent years. Bradley (1972, 1974) grouped these mechanisms into 3 general catagories: Type 1, populations determined by transmission; Type 2, populations regulated at the host population level by immunological and pathogenic processes; and Type 3 regulation at the individual host level by premunition and other immune processes. It can be assumed that B. monandros transmission rates are usually well above the minimum for mere persistence of the parasite because young cockroach nymphs have high infection intensities. Subsequently, efficient regulation is achieved by control of each infrapopulation at the level of the individual host (Type 3) and parasite loads remain relatively stable.

An aggregated or overdispersed pattern of parasite distribution seen in most host-parasite systems (Anderson, 1982c; Anderson & Gordon, 1982; Bradley, 1974) is not demonstrated by B. monandros. Rather, this parasite has an underdispersed distribution pattern. In highly aggregated parasites, it is in those few hosts having most of the

parasites that density-dependent regulation (by host death) of parasite abundance is most severe; such regulation acts to constrain the growth of the parasite suprapopulation (Anderson, 1982,c). Density-dependent regulation may also occur in parasites where aggregation is low to random if levels of pathogenicity are high. In B. monandros, regulation of abundance is also density-dependent in each host and affects both the prevalence and mean intensity of the nematodes in the host population as a whole.

C) REPRODUCTIVE COMPETITION AND CYCLICAL EGG PRODUCTION IN THELASTOMATID NEMATODES OF COCKROACHES

Abstract

The nematode Blatticola monandros Zervos lives in the hind gut of the cockroach Parellipsidion pachycercum Johns. The modal infrapopulation type consists of one adult male and one adult female nematode. A few hosts have two adult females. Single adult female nematodes in adult cockroach hosts produce more eggs than the total produced by two females when two are present in a host. Eggs are produced cyclically with short periods of high egg production interspersed with several days of very low or no egg production. Most eggs produced on any one day are attached on the outer surface of only one of the up-to-six faecal pellets produced by the host per day. Mechanisms which may control reproductive competition and cyclical egg production are discussed.

INTRODUCTION

Blatticola monandros Zervos, 1983 (Oxyuroidea: Thelastomatidae; Section III, C) lives in the hind gut of the endemic New Zealand cockroach Parellipsidion pachycercum Johns, 1966 (Blattellidae). The size and structure of nematode infrapopulations are regulated through a density- and sex-dependent reduction in number which results in a predominance of monogamous infrapopulations in older hosts (Section IV, B). No host contains more than one adult male, a few (9.3% in adult hosts) have two adult females both of which are smaller than females from a monogamous pair (Section IV, B). In this paper, I present evidence that lone adult females are more fecund than is each female or both females together when two are present and I also show that eggs are produced cyclically and in batches.

METHODS

Adult P. pachycercum were collected from the bark on trunks of fuchsia trees (Fuchsia excorticata (J. R. et G. Forst.) Linn. f.) growing within 10 m of the stream at the end of the Kaituna Valley road, Banks Peninsula, Canterbury, New Zealand (43°43'15" S, 172°45'30"E; elevation 250m) on three occasions in 1983 (24 July; 18 September; 20 October). On each date forty cockroaches were isolated in individual containers and each was provided with abundant food and water. To ensure that the diet of each cockroach was similar, only rabbit pellets (diet 94P, H. Archer and Son, Christchurch) were given to each. Faecal pellets produced by each cockroach were collected daily for a period of 30 days, placed on separate slides, examined with a stereo microscope, teased out in saline and examined with a compound microscope. The number and disposition of B. monandros eggs were noted. Uninfected cockroaches (operational definition: no eggs passed within 7 days of the start of the observations) or cockroaches that died were replaced by another individual collected on the same date. Data from one cockroach which passed an adult female nematode on day 26 of the observations are excluded. For each cockroach, B. monandros infrapopulation composition was determined by dissection on day 30. Values for k (dispersion parameter) for the negative binomial distribution of eggs were calculated by iteration using the method in Southwood, 1978 (method 2, p 28). All ecological terms used are defined by Margolis et al. (1982).

RESULTS

i) Productivity of female nematodes

Most (107) of the 119 cockroaches had a single adult female Blatticola monandros with an adult male. The remainder (12) had 2 adult females per infrapopulation. Assuming equal fecundity per female,

female nematodes produced fewer eggs each if accompanied by another female than if alone (t = 11.975, $P < 0.001$; Table 6.). In addition, total egg output by 2-female-infrapopulations was lower than that by single-female-infrapopulations (t = 8.758, $P < 0.001$; Table 6.). No significant differences were found between the mean number of eggs produced by single female nematodes in male and female hosts (t=0.467, $P > 0.1$). Therefore, these data were combined (Table 6.). Data from male and female hosts containing 2 female nematodes are also combined (Table 6.) because the number of female hosts with 2 female nematodes (3) was small.

ii) Periodicity of egg laying

Nematode eggs on the faeces of cockroaches appeared cyclically with short periods of high egg appearance interspersed with several days of very low or no egg appearance (Fig. IV, C, 1). Fractional values of k (dispersion parameter) were the most common (Table 6.) and all except one (k= 3.138) were below 3. Periodicity of egg appearance on faecal pellets from hosts with one adult female was similar for both male and female hosts (number of egg-free days t = 0.757, $P > 0.1$; Table 6.), although cycle period differed between different hosts and was not temporally constant for each idiohostal unit (Fig IV, C, 1). When 2 adult female nematodes were present in a host, eggs appeared on fewer days (t= 5.701, $P < 0.001$) than if only 1 was present (Table 6.), but these eggs still appeared cyclically (comparison of k values: t= 0.213, $P > 0.1$; Fig. IV, C, 1). The total number of eggs passed on any peak production day by 2 female nematodes in one host was always less than the number passed by 1 female on her day of maximum production. The maximum number of eggs passed on 1 day by a host with 1 adult female nematode was 28. Most eggs passed on peak days were found on only 1 of

	Eggs / day			*k* values				Number egg-free days*		
	Mean eggs per female nematode	S.D.	Range eggs per female nematode	Mean	S.D.	Range	% hosts with *k*<1	Mean	S.D.	Range
A	3.60	0.82	1.35-5.30	0.66	0.41	0.27-3.14	93.5	9.80	2.43	2-17
B	0.77	0.11	0.60-0.95	0.68	0.24	0.24-1.15	83.5	13.90	1.88	12-19

Table 6. Faecal egg count data from Blatticola monandros in adult Parellipsidion pachycercum. A, hosts with 1 adult ♀ nematode; B, hosts with 2 adult ♀ nematodes; *, number of days eggs absent from cockroach faeces.

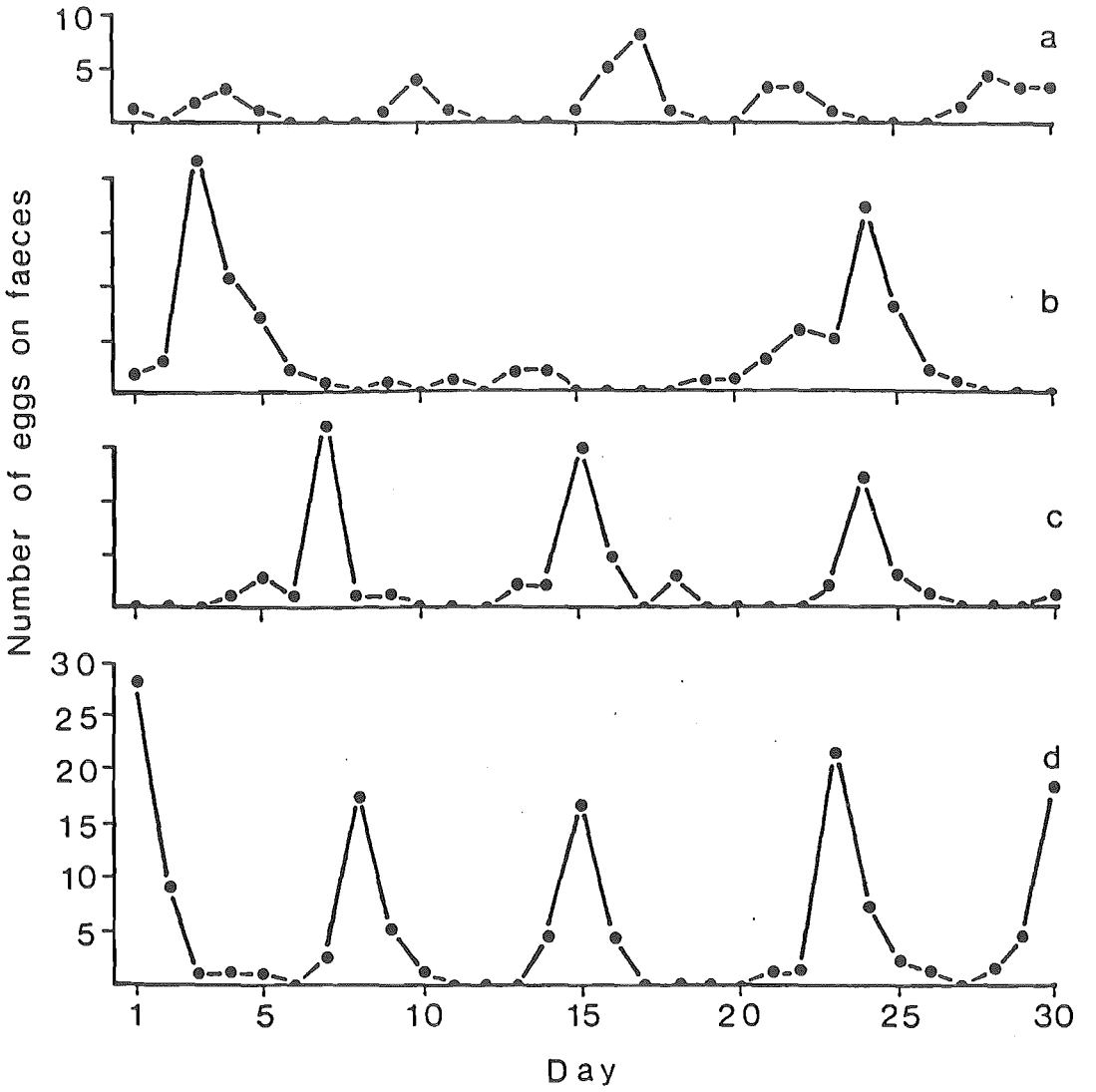


Figure IV, C, 1

Representative examples of egg production periodicity by Blatticola monandros in adult Parellipsidion pachycercum.

(a), total egg production from host (female) containing 2 adult female nematodes ($\underline{k}$= 1.0);

(b-d), long, medium and short cycle period of production by single female nematode per host; (b), female host ($\underline{k}$= 0.576); (c), male host ($\underline{k}$= 0.398); (d), female host ($\underline{k}$= 0.516).

the up-to-6 faecal pellets produced by the host. All eggs were on the outer surface of faecal pellets. Female nematodes released into saline by dissection of the host laid up to 30 eggs within about 5 minutes.

DISCUSSION

Single female Blatticola monandros produce more than 4 times as many eggs than do females when two females are present in a single host (Table 6.). Reasons for this reduction in fecundity of crowded females are unknown, but competition for a limited food resource is a possibility. When two females are present in an infrapopulation, both are smaller than lone females (Section IV, B). Fecundity may be proportional to size and size may be reduced by competition for nutrients. Alternatively, reduced egg production may result from chemical interference, either active or passive. Active chemical interference could involve the production of some inhibitory substance by one or both females. The reduction in infection intensity observed in B. monandros may involve such an inhibitory substance (Section IV, B). In most cases, only one adult female survives (together with an adult male). Where two females survive, it is possible that neither is capable of eliminating the other and that any mutually inhibitory substance produced may act only to reduce fecundity. Passive chemical interference could occur if wastes produced by two females exceed some level, after which they act as toxins which reduce egg production.

It seems likely that both females in two-female infrapopulations suffer this loss in fecundity. Both immediately deposit eggs when released in saline by host dissection and both could therefore be expected to lay a proportion of those eggs found on faecal pellets. Even if only one female of two present in an infrapopulation lays eggs

in a host, egg output is still lower than that of single females.

Egg production is cyclical and especially pronounced in infrapopulations where only one adult female is present. Values of $k < 3$ indicate clumped egg production and values below 1 indicate a highly clumped distribution (Southwood, 1978). Most k values were <1 and only one was marginally above 3. Cyclical egg production was enhanced by clumping the majority of eggs produced on one day on only one of several host faecal pellets.

There may be several causes of batch egg production. For example, the reproductive cycle and egg deposition behaviour of these nematodes may be under the control of some host hormonal cycle or activity. If this is true, peak egg production by lone female nematodes and apparent synchronous peak egg production by both females when two are present may occur at a particular stage in the host cycle. Although reproductive cycle period was not determined for female *P. pachycercum*, it can be assumed that, as in other cockroaches (Bell & Adiyodi, 1982), large and predictable changes in corpora allata activity and hence in hormone synthesis and release occur during the female gonotrophic cycle. Such changes may account for reproductive periodicity of *B. monandros* in adult female hosts but would not explain the almost identical phenomenon in males. In other cockroaches, for example *Leucophaea maderae*, corpora allata activity in males is maintained at a fairly constant, low level throughout adult life (Scharrer & von Harnack, 1958) and has no effect on the maintenance of reproductive activity (Scharrer, 1946). Host hormonal cycle control of *B. monandros* reproductive behaviour is therefore unlikely. To date there seems to be no well-documented instance of synchronization between any entomophilic nematode and the hormonal milieu of its host (Riddiford, 1975). Nadakal

& Nayar (1968) did report that the lack of corpora allata hormone reduced fecundity of three unidentified hind gut thelastomatids in the cockroach Periplaneta americana L. but their evidence was inconclusive (Gordon, 1970; Hominick & Davey, 1972 a,b) and they gave no information concerning daily egg output.

Alternatively, batch egg laying may be dictated by the physical form of the female reproductive structures. The capacity of the uterus is probably limited, and, given a developmental delay in egg production, batches of eggs would be produced periodically. Batch production of eggs may result from limited sperm availability. If females mate more than once, it is possible that a limited amount of sperm is passed each time and that synchronously developing eggs are retained until a certain stage in development, then released together. Or, there may be time delays in mate finding, mating, and/or subsequent egg development.

Whatever the cause, female B. monandros lay a group of eggs, rather than spread egg laying equally over time. These nematodes are dioecious and batch egg production may enhance reproductive success because it is more likely to lead to both a male and a female becoming established in the next host. Most oxyuroids produce eggs in batches (Adamson, 1983). In some oxyuroids, eggs are clumped by sticky coats, sticky secretions, or by interlocking filaments (Basir, 1948, 1951; Jarry, 1964; Lee, 1961; Leibersperger, 1960; Sanchez, 1945; Van Waerebeke, 1978). In others, eggs are encapsulated in two's and three's within the same shell, or are produced in a tube, or the entire egg-containing female is passed out with the faeces of the host (Basir, 1956; Hugot, Bain & Cassone, 1982; Seurat, 1920, cited by Adamson, 1983).

Most parasites have an overdispersed (aggregated) distribution pattern (Anderson, 1982a, c; Anderson & Gordon, 1982; Bradley, 1974).

For these parasites, spatial clumping of infective stages is a major determinant of overdispersion (Anderson, 1982a; Crofton, 1971; Keymer, 1982; Keymer & Anderson, 1979). B. monandros however, is unusual in having an underdispersed (regular) distribution pattern in the host (Section IV, B). Consequently, spatial clumping of infective stages does not lead to overdispersion because the progeny of most eggs initially or subsequently ingested fail to establish or survive to maturity (Section IV, B).

The negative effect of density-dependent intraspecific competition on various population parameters in parasitic helminths - the "crowding effect" - has been known for some time (see Halvorsen, 1976; Kennedy, 1975, for reviews). Amongst parasitic nematodes, an inverse relationship between infection intensity and per capita fecundity has been noted for a number of species (for examples, see Croll, Anderson, Gyorkos & Ghadirian, 1982; Dunsmore, 1960; Krupp, 1961; Michel, 1967; Yong & Dobson, 1982). However, it is unclear if reduction in fecundity of crowded parasites is caused by competition between parasites, by the immune responses of the host, or both (Kennedy, 1982). Control of gut parasites by immune responses in invertebrate hosts is unknown (Lackie, 1980) and can be discounted as a cause of reduced fecundity in such parasites. Thus in B. monandros reduced fecundity probably results from some kind of competition between adult females when two are present.

D) SEASONALITY OF THELASTOMATID NEMATODES IN A FIELD POPULATION OF COCKROACHES

Abstract

The monogamous nematode Blatticola monandros lives in the hind gut of the endemic New Zealand cockroach Parellipsidion pachycercum. This nematode is underdispersed due to density- and sex-dependent reduction of infection intensity in each host. Seasonal variations in incidence and infrapopulation structure were slight over a three year period, except during one unseasonably dry summer. During the drought, incidence of monogamous infrapopulations and transitional infrapopulations was lowest, while incidence of single worm and single sex infrapopulations was greatest. Drought related factors reduced transmission below the level at which density-dependent regulation normally operates in the parasite population.

INTRODUCTION

Blatticola monandros Zervos, 1983 (Oxyuroidea: Thelastomatidae; Section III, C) occurs in the hind gut of the endemic New Zealand cockroach Parellipsidion pachycercum Johns, 1966 (Blattellidae). The cockroach has six nymphal classes (probably instars) of increasing size (defined as size classes 1-6) and one adult class which occur throughout the year (Section II, B). The nematode has a direct life cycle and, at the collection site (Kaituna Valley), it occurs only in P. pachycercum (Section III, Section IV, B). Infection incidence is high (54% in smallest nymphs; 92% in penultimate nymphs), but there is an inverse relationship between nematode intensity and host age because of density- and sex-dependent reduction in nematode numbers

which results in a unimodal, monogamous, infrapopulation type (Section IV, B). Other infrapopulation types, which are probably transitional to this unimodal type, may include up to four adult females and/or up to seven juvenile females but never more than one adult male. Infrapopulations including two juvenile males are very rare (0.15% of all infrapopulations; Section IV, B). The present study reports the results of a three-year survey of field collected hosts to determine if seasonal fluctuation occurred in the B. monandros population.

METHODS

Nymphs and adults of P. pachycercum (n=4135) were collected from the bark on trunks of fuchsia trees (Fuchsia excorticata (J.R. et G. Forst) Linn.) growing within 10m of the stream at the end of the Kaituna Valley Road, Banks Peninsula, Canterbury, New Zealand ($43^{o}43'15"S.$, $172^{o}45'30"E.$; elevation 250 m). Collections were made once every five weeks from 1 March 1981 to 21 February 1982, then sporadically until 14 February 1984. Cockroaches were killed by crushing the nerve cord behind the head, assigned to a size class, and dissected in cockroach saline. The number, developmental stages, and sexes of nematodes in each infrapopulation were noted. Infrapopulations in adult male and adult female hosts are considered together as there is no significant difference in infection between sexes (Section IV, B). B. monandros suprapopulation and infrapopulation structures are described in Section IV, B and all ecological terms used are defined by Margolis et al., 1982.

RESULTS

i) Infection incidence

The seasonal incidence of B. monandros in P. pachycercum is given in Fig. IV, D, 1. During one summer (1981-1982), incidence was

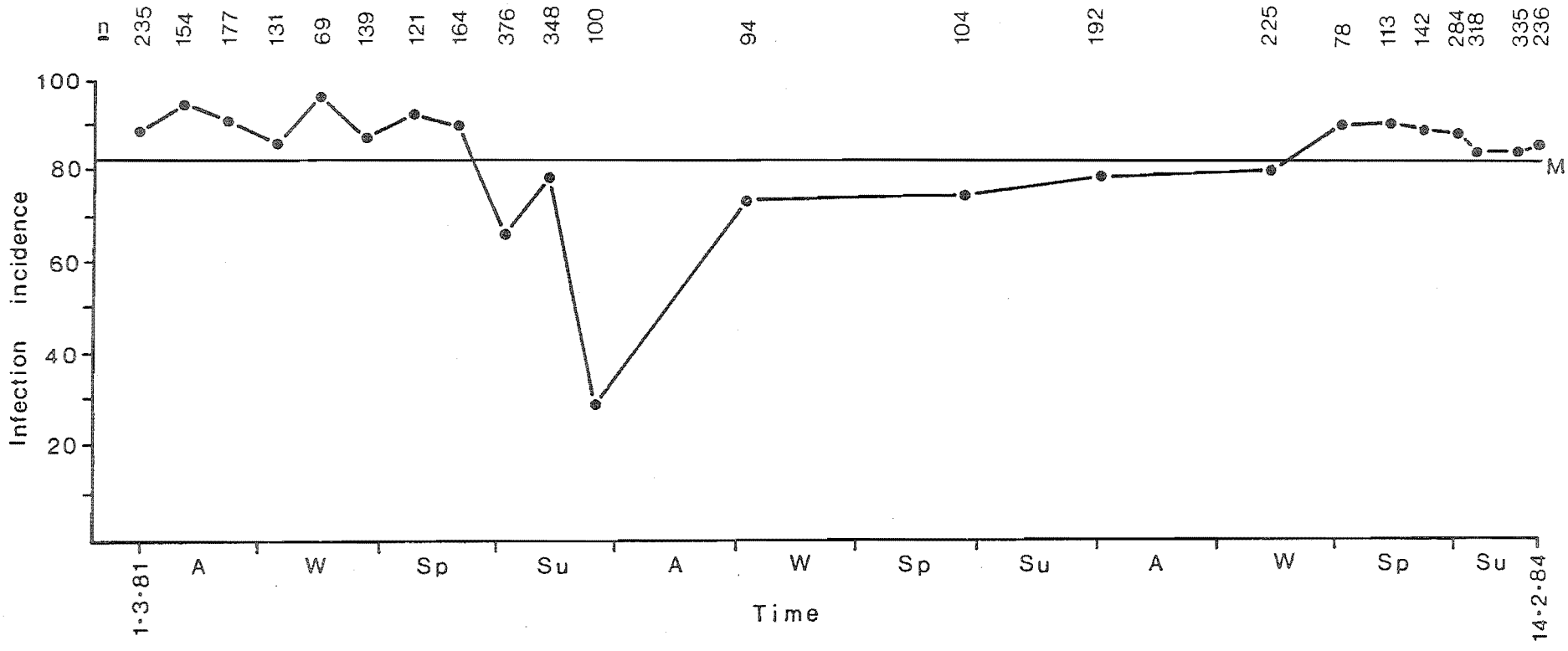


Figure IV,D,1. Infection incidence of B. monandros in P. pachycercum (n = 4135) over a three year period. Time divided into 5-week intervals. New Zealand seasons: spring (Sp), 1 September - 30 November; summer (Su), 1 December - 29 February; autumn (A), 1 March - 31 May; winter (W), 1 June - 31 August. First collection date, 1.3.81; last collection date, 14.2.84. M, mean infection prevalence. n collected on each date, above graph.

lower than the mean (82%), especially in February. Similarly, within each size class of host, incidence was lower than the size class mean during summer 1981-1982. No size class 1 host was infected with B. monandros in February, 1982. After that summer, at least one year elapsed before incidence again approximated the mean.

ii) Seasonal infrapopulation structure

The incidence of various infrapopulation types varied throughout the collection period. Monogamous infrapopulations were established in smallest hosts (size class 1) only in summer and early autumn, 1981 and 1983-1984. However, monogamous infrapopulations occurred in larger hosts in all seasons except during the summer of 1981-1982 when incidence of monogamous infrapopulations was below the size class mean for this type in each class. In comparison, more single sex and single worm infections occurred during summer 1981-1982. Infrapopulations composed of juvenile female(s) with an adult male (transitional infrapopulations) were usually common in smaller nymphs. However, during February 1982, only one cockroach (in size class 2) had an infrapopulation of this type. At other times, fluctuations of the above four infrapopulation types were apparently random. Infrapopulations which included juvenile male(s) were rare (2.2% of all infrapopulations) but occurred in most months, mainly in smaller cockroaches.

DISCUSSION

In spite of spatial clumping of the infective stage (eggs) (Section IV, C), the population of Blatticola monandros in Parellipsidion pachycercum is underdispersed (regular) and generally stable because of density- and sex-dependent reduction of infection intensity in each infrapopulation with host age (Section IV, B). This regulation is similar to Bradley's (1972,1974) Type 3 regulation

(Section IV, B). It determines infrapopulation structure and the upper limit of infection intensity. Host immunological control and/or B. monandros virulence can both be discounted as causes of population regulation in this nematode (Section IV, B). It seems likely therefore, that changes in the B. monandros population during summer 1981-1982 were related to unseasonably low rainfall (only 44% of the local mean; Christchurch Meteorological Office) during that time. Drought is one of many density-independent factors which determine parasite population size (Bradley Type 1 regulation). In B. monandros, drought apparently reduced transmission below the point at which the normal density-dependent factors act in a regulatory manner. After one year, the population of this nematode returned to a prevalence, intensity and infrapopulation distribution similar to that seen prior to the drought.

During the drought, transmission and/or retention of nematodes may have been reduced. Possible causes for reduction in transmission may include decreased egg survival and/or decreased egg intake. Thelastomatid eggs lose water and collapse when exposed to experimental desiccation, (Wharton, 1980) and could be expected to respond similarly in the field. Alternatively, it is possible that cockroaches in all classes were stressed through lack of water during the drought. Dehydrated cockroaches do not feed (Bell & Adiyodi, 1982, p.123). If P. pachycercum was drought-stressed, its consumption of B. monandros eggs on faecal pellets may have declined. Established B. monandros infrapopulations may have also been stressed as a consequence of changes in host diet. In Periplaneta americana for example, juvenile hatching and retention of adult thelastomatids are both affected by host diet (Hominick & Davey, 1972b; Peregrine, 1974). Hence changes in the diet of P. pachycercum during the drought may have caused stress amongst its

nematodes which in turn may have contributed to the changes observed in the nematode population. Amongst parasites in general, there is ample evidence that stress in a host or a potential host may alter host carrying capacity or recruitment of parasites (Esch, Gibbons & Bourque, 1975).

E) POPULATION REGULATION IN FOUR SPECIES OF PARASITIC THELASTOMATID NEMATODES OF COCKROACHES

Abstract

Four species of thelastomatid nematodes in six cockroach species have populations regulated by a density- and sex-dependent reduction in nematode numbers per host. No host contained two males, the number of adult females per host was small, and monogamy was common. Juvenile males were rare while juvenile females were relatively common, indicating that, compared to females, males develop and are eliminated rapidly from hosts (leaving one). Infection prevalence varied markedly between the species.

INTRODUCTION

The population of a thelastomatid nematode (Blaticolla monandros Zervos, 1983, Nematoda: Thelastomatidae; Section III, C) in the hind gut of a blattellid cockroach (Parellipsidion pachycercum Johns, 1966, Blattellidae) is regulated through a density- and sex-dependent selective reduction in infection intensity with infrapopulation age (Section IV, B). It has a modal infrapopulation type consisting of one adult male and one adult female, juvenile males are uncommon, infrapopulations with two juvenile males are very rare, and no host containing two adult male nematodes has been found (Section IV, B). Similarly, the thelastomatid Protrellus dixoni Zervos, 1986, (Section III, D) in the cockroach Drymaplaneta variegata (Shelford, 1909) never has more than one adult male and only a few adult females per host (Section III, D).

To determine if similar population structures are common amongst thelastomatids in cockroaches, a number of cockroach species were examined and their nematode populations analysed. These were Protrellus dalei Zervos (Section III, E) in Celatoblatta peninsularis Johns,

1966, C. vulgaris Johns, 1966, and C. brunni (Afken, 1901) Johns, 1966; Blatticola barryi Zervos (Section III, E) in C. quinquemaculata Johns, 1966; B. blattae (Graeffe, 1860) Chitwood, 1932 in Blattella germanica L.; and Suifunema mackenziei Zervos (Section III, E) in C. undulivitta (Walker, 1868) Johns, 1966. Like B. monandros and P. dixoni, males of these species are markedly smaller than females (Chitwood, 1930; Section III, E).

METHODS

C. peninsularis were collected once every five weeks from Kaituna Valley, Banks Peninsula, New Zealand, from 1 March 1981 to 21 February 1982, as described in Zervos, 1984 Section II, B). Other Celatoblatta species were collected sporadically during 1981-1984 from sites described in Section III, E. Blattella germanica (Section II, E) were collected from a suburban garden, St. Lucia, Brisbane, Australia, during September-October 1984, and preserved in formalin prior to shipment to Christchurch. Other cockroaches were killed after collection by crushing the nerve cord behind the head. Nymphs of C. peninsularis were assigned to 6 sub-adult size classes (Zervos, 1984; Section II, B)) and nymphs of C. vulgaris to 5 sub-adult size classes (Section II, C) on the basis of minimum interocular distance and hind femur length. Small nymphal collections of the other 4 cockroach species precluded nymphal size classing. Such nymphs, which were large and probably sub-adult, are here included as adults.

Cockroaches were dissected and their nematode infrapopulations noted. Some newly moulted and still untanned sub-adult and adult Celatoblatta peninsularis and C. vulgaris were among those dissected. Analyses were made of populations of P. dalei in C. peninsularis and C. vulgaris at the different developmental stages of these hosts.

Analysis of the remaining populations was restricted to those in adult hosts. Measurements were made of some adult P. dalei from size class two nymphs (n nematodes measured= 4) and adult (n= 11) C. peninsularis. Population terminology follows that of Margolis et al., 1982. Thus a suprapopulation consists of all individuals of a given parasite species in all stages of development within all hosts in a particular ecosystem, whereas those in an individual host constitute an infrapopulation.

RESULTS

i) Introduction

Infection data for each nematode species is presented in Table 7. Nematodes were found in the anterior part (colon) of the hind gut with the male alongside or anterior to the anteriorly directed head of the female(s). No cockroach had more than one adult or juvenile male (none had both) and the number of adult females/host was small (usually 1-2, but up to 4). In all suprapopulations, females were more numerous than males, adults were more numerous than juveniles, and adult females were more numerous than adult males (with the exception of P. dalei in C. peninsularis, where adult males were more numerous than adult females). Juvenile females were often numerous in an infrapopulation (up to 7/host) when adult females were absent. When adult females were present, juvenile females were scarce. Few juvenile males were found.

ii) Protrellus dalei in Celatoblatta vulgaris and C. peninsularis

Infection prevalence (Fig. IV, E, 1) was low in small nymphs, rose in penultimate and ultimate nymphs in C. vulgaris only, but was highest in adults of both host species. Newly moulted cockroaches contained adult nematodes.

Table 7. Infection data for thelastomatid nematodes in *Blattella germanica* and *Celatoblatta* species. C, cockroach species name (A, *Celatoblatta vulgaris*; B, *C. peninsularis*; C, *C. brunni*; D, *C. quinquemaculata*; E, *C. undulivitta*; F, *Blattella germanica*); n, number collected; I, % infected; P, name of thelastomatid (A, *Protrellus dalei*; B, *Blatticola barryi*; C, *Suifunema mackenziei*; D, *Blatticola blattae*). Nematode infrapopulation types (as a % of infected hosts only): 1, 1 adult male (= am) + 1 adult female (= af); 2, 1 am + juvenile female(s) (= jf(s)); 3, jf(s) only; 4, 1 am; 5, af(s) only; 6, 1 am + 2^{+} af; 7, miscellaneous (1 am + af(s) + jf(s); af(s) + jf(s); juvenile male +/- f(s)). R, sex ratio (m:f) of nematodes in each suprapopulation (upper figure, all nematodes; lower figure, adult nematodes).

C	n	I	P	Nematode infrapopulation type							R
				1	2	3	4	5	6	7	
A	445	35.7	A	30.0	3.8	11.4	17.1	24.0	5.7	5.7	1:1.95 1:1.3
B	768	4.8	A	10.8	5.4	10.8	46.0	13.5	–	13.5	1:0.9 1:0.44
C	35	65.7	A	52.2	8.7	–	17.4	17.4	4.3	–	1:1.26 1:1.1
D	30	93.3	B	42.9	–	–	–	46.4	7.1	3.6	1:2.4 1:2.4
E	28	64.3	C	33.3	–	–	33.3	11.0	5.5	16.7	1:1.92 1:1.2
F	36	94.4	D	64.7	–	2.9	5.9	17.7	8.8	–	1:1.4 1:1.3

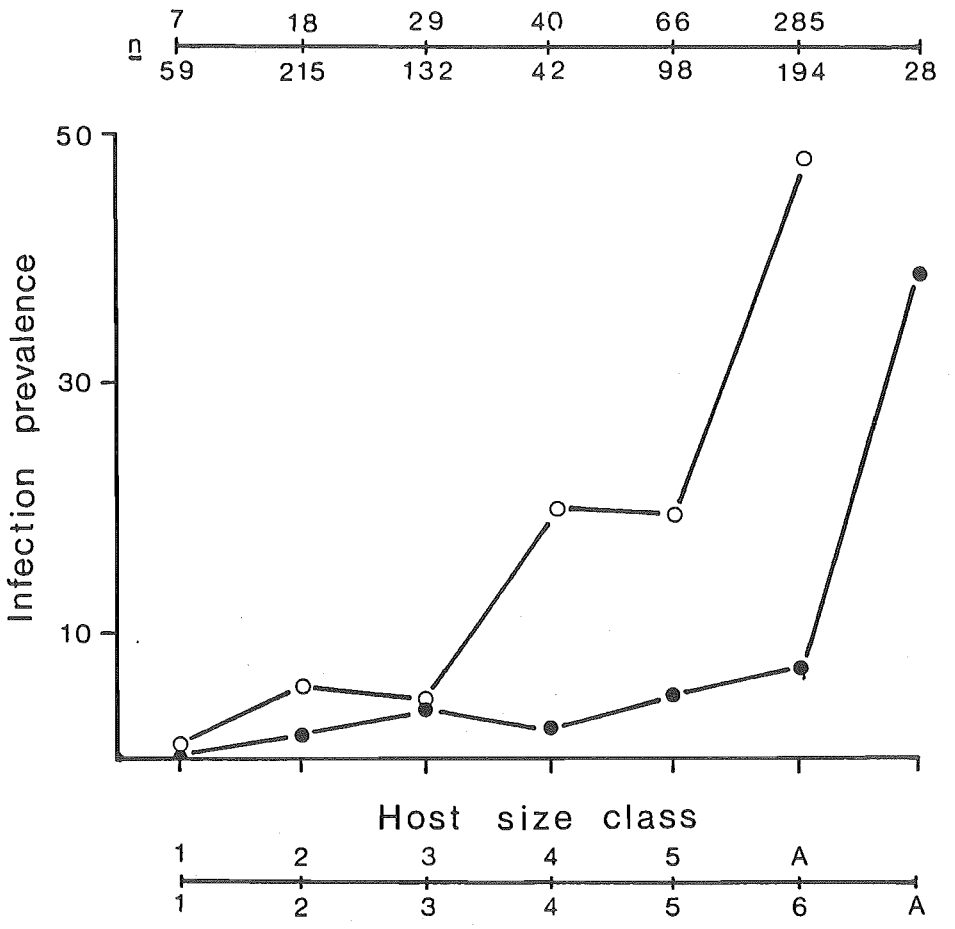


Figure IV, E, 1

Percentage in each size class of Celatoblatta peninsularis (solid circles) and C. vulgaris (open circles) infected with Protrellus dalei.

Host size class 1-5 (C. vulgaris, upper line) and 1-6 (C. peninsularis, lower line), nymphs; A, adults. Total cockroaches per class (n) above graph (upper line C. vulgaris; lower line, C. peninsularis).

The modal infrapopulation type in C. vulgaris consisted of 1 adult male and 1 adult female (monogamous infrapopulations, Table 7). Infrapopulations with a single adult male, with or without juvenile and/or adult female(s) comprised over half of all infrapopulation types. Remaining infrapopulations comprised mainly juvenile and/or adult female(s) without a male. Only 7 C. vulgaris contained a juvenile male, alone or with juvenile females.

The modal infrapopulation type in C. peninsularis consisted of a single adult male only, while monogamous infrapopulations were only one third as numerous as in C. vulgaris. No host contained more than one adult female. Adult nematodes of both sexes were smaller in nymphs and female nematodes contained fewer eggs (in size class 2 C. peninsularis, adult male nematodes were 630+/-29 um and the only adult female found was 2480um long, but adult males were 1067+/- 35um and adult females 4323 +/- 149 um long in adult hosts). Adult females occurred in smaller nymphs only if an adult male was present, whereas single adult males were found in class 2 (and older) nymphs. Adult females without a male were found only in sub-adult and adult cockroaches. Juvenile females, when present, were most numerous in smaller cockroaches and few occurred in sub-adult or adult hosts. Only 2 C. peninsularis (both size class 5 nymphs) contained a juvenile male (each with a juvenile female).

iii) Protrellus dalei in Celatoblatta brunni;
Blatticola barryi in C. quinquemaculata;
B. blattae in Blattella germanica;
Suifunema mackenziei in C. undulivitta

In P. dalei and B. blattae, the modal infrapopulation type was a monogamous pair (Table 7). While monogamous infrapopulations were common in B. barryi and S. mackenziei, single sex infrapopulations

common in B. barryi and S. mackenziei, single sex infrapopulations were the modal infrapopulation type. Single sex infrapopulations were also common in P. dalei and B. blattae. Juvenile females were scarce and no juvenile males were found.

DISCUSSION

These results indicate that Protrellus dalei, Blatticola barryi, B. blattae, and Suifunema mackenziei resemble Blatticola monandros in Parellipsidion pachycercum in that their infrapopulation size and structure is regulated through a density- and sex-dependent selective reduction in infection intensity. Evidence for regulation can be inferred from the data because in spite of the comparatively small size of adult males, monogamy is common and never more than one male/host occurs. Also, while numerous juvenile females may occur in one host when adult females are absent, only one or two adult females are found. The scarcity or absence of juvenile males but relative abundance of juvenile females suggests that males develop more rapidly than females and that male elimination occurs more rapidly than female elimination.

Like B. monandros (Section IV, B), adult P. dalei are retained through the moults of C. peninsularis and C. vulgaris and increase in size with increasing host size in C. peninsularis (and probably in C. vulgaris). Thus older (larger) C. peninsularis have the capacity to support an increased parasite biomass. This capacity never results in more than one adult male and/or one adult female. If juvenile females are present, they are usually numerous in smaller nymphs or in the absence of adult female nematodes.

The results obtained for Blatticola blattae in Blattella germanica are similar in some respects to those found by Chitwood (1930) and Bozeman(1942). However, both sometimes found two males per host.

Chitwood (1930) gave no further information concerning intensity of males but Bozeman (1942) found two male nematodes only in female and unsexed (presumably immature) cockroaches. Nevertheless, the average number of male worms per host was low (0.64-0.7/host, Bozeman, 1942). In comparison, no B. germanica from Brisbane contained more than one adult male. It is possible that Chitwood and Bozeman mistook juvenile males for adults. In most oxyuroids, males are sexually precocious (Adamson & Petter, 1983a) and in some, juvenile males closely resemble adult males because, although lacking gonads, they have a spicule and adult-like tail (Section III, C, D, E). Although no case of two juvenile males per host occurred in any of the nematodes discussed in this paper, two juvenile males per host have been reported in a thelastomatid (Section IV, B).

There are several possible regulatory mechanisms which could lead to the distribution patterns observed in these nematodes. These mechanisms were discussed (and most were discounted) in Section IV, B. Experimental evidence using another thelastomatid (Section IV, F) indicates that self-regulation probably controls populations of the thelastomatid concerned. Self regulation may also occur in the thelastomatids considered in this paper.

Infection prevalence varied markedly amongst these cockroaches. Prevalence of P. dalei in C. peninsularis was very low compared to prevalence of the same nematode in other hosts, prevalence of other nematodes discussed here, and prevalence of thelastomatids in other wild collected cockroaches. For example, 81% of P. pachycercum collected from the same site as C. peninsularis (Kaituna Valley) over a three year period were infected with B. monandros (Section IV, B), and 55% of Drymaplaneta variegata collected from Hexton, Gisborne were infected with Protrellus dixoni (Section III, D). Dale (1966) found 86% of

Platyzosteria novaeseelandia (Brunner v. Wattenwyl, 1865) infected with Blatticola tuapakae Dale, 1966 and/or Protrellus gurri (Dale, 1966) Zervos, Section III, D. High infection prevalence (about 75-90%) is also common in a variety of cockroach species collected from dwellings and laboratory rearing cages (for example, see Bozeman, 1942; Chitwood, 1930; Dobrovolny & Ackert, 1934; Todd, 1944; Tsai & Cahill, 1970). C. peninsularis may be an unusual host for P. dalei, and this nematode may be struggling to survive in this cockroach. Evidence for this is that there are a large number of non-reproductive (i.e., male only) infrapopulations in C. peninsularis, and infection prevalence is highest in adult cockroaches, which are scarce or absent throughout most of the year (Zervos, 1984; Section II, B).

Like female Blatticola monandros (Section IV, B), female P. dalei in C. peninsularis apparently do not develop to adulthood in small cockroaches unless a male is present. Males may provide some stimulus to female development without which female development is delayed. Lone female nematodes in all species contained eggs with developing juveniles. Possibly the male was lost to the infrapopulation, or females may be facultative parthenogenes.

F) EVIDENCE FOR POPULATION SELF-REGULATION, REPRODUCTIVE COMPETITION AND ARRHENOTOKY IN A THELASTOMATID NEMATODE OF COCKROACHES

Abstract

Experimental infection of adult Drymaplaneta variegata (Blattodea) with known numbers of eggs of Protrellus dixoni (Nematoda: Thelastomatidae) showed that each infrapopulation was regulated by a density- and sex-dependent reduction in infection intensity with infrapopulation age. This reduction was not equal in initial speed or intensity between the sexes (reduction in number of males was faster) and led to infrapopulations with never more than a single adult male, 1 - 8 (usually 1 - 3) adult females and 0 - 28 juvenile females. In structure, these laboratory produced infrapopulations resembled those in field collected hosts. Infrapopulation regulation was probably due to parasite-mediated chemical interference competition and benefited remaining nematodes because per capita fecundity was greater in uncrowded worms. Unmated females produced male offspring only (probably by arrhenotokous parthenogenesis). Only females that had access to a male produced females, although they also produced males; such females may avoid insemination or prevent fertilisation of some or all eggs. Female offspring probably result from amphimixis.

INTRODUCTION

Analysis of a population of Blatticola monandros Zervos, 1983 (Oxyuroidea: Thelastomatidae; Section III, C) from field-collected Parellipsidion pachycercum Johns, 1966 (Blattodea: Blattellidae) showed that 1), infrapopulations of B. monandros are controlled through a density- and sex-dependent reduction in infection intensity with host age; 2), monogamous infrapopulations predominate in older cockroaches;

3), never more than one adult male per host is found; 4), uncrowded nematodes have a greater per capita fecundity (Section IV, B, C). Other thelastomatid species in other cockroach species also have populations regulated by density- and sex-dependent reduction in infection intensity (Section IV, E). It was suggested (Section IV, B, E) that regulation was the result of the production of some anthelmintic(s) by the nematodes present in an infrapopulation. Laboratory investigation of self-regulation by B. monandros proved impracticable because P. pachycercum could not be bred or handled easily in the laboratory. Instead, experimental evidence for density- and sex-dependent population self-regulation, thought to be widespread amongst thelastomatids (Section IV B, E), was obtained using a more readily cultured thelastomatid-cockroach model (Protrellus dixoni Zervos, Section III, E in Drymaplaneta variegata (Shelford, 1909)). Evidence for the effect of crowding on fecundity, for arrhenotokous parthenogenesis (the production of males from unfertilised eggs and females from fertilised eggs) and for haplodiploidy (the existence of haploid males and diploid females) was also obtained.

MATERIALS AND METHODS

i) Cockroach

Drymaplaneta variegata (identified by Mr. P.M. Johns, Department of Zoology, University of Canterbury, Christchurch, New Zealand) were collected on several occasions between June 1982 and August 1983 from outbuildings and woodpiles on a farm at Hexton, Gisborne, North Island. Some adults (23 female, 48 male) were dissected and examined immediately for nematodes to determine infection prevalence and intensity in wild hosts (Section III, D). Most female cockroaches were retained for breeding purposes. Naive laboratory colonies were set up as follows:

A few adults (mostly females) were kept in plastic biscuit barrels with a variety of foods and water. Deposited oothecae were removed daily, cleaned with cotton wool soaked in 10% methanol to remove any adhering nematode eggs, and transferred to clean plastic lunch boxes with food and water ad lib but without adults. A week after oothecae hatched, 25-50% of the nymphs were dissected and examined for nematodes. The remaining nymphs were used to establish naive colonies in two cockroach nymph-proof wood and glass colony boxes (dimensions: 50 x 50 x 60 cm). Two similar colony boxes contained infected cockroaches (established from adults and nymphs collected at Hexton). All colonies were provided with abundant food and water. One year later, each colony contained several hundred cockroaches. At 2 - 3 month intervals during the course of the experiments which followed, 10 - 20 cockroaches from each naive colony were dissected to confirm the continued absence of nematodes.

ii) Nematode

Protrellus dixoni inhabits the anterior hind gut of Drymaplaneta variegata, has a direct life cycle, and is sexually dimorphic (Section III, D). Juvenile males are distinguishable from juvenile females by their fully developed spicule (but only developing gonads) and a truncate not elongate tail.

INFECTION EXPERIMENTS

Naive adult cockroaches of both sexes, individually isolated in clean plastic lunch boxes, were used throughout the experiments. They were denied food and water for 24 hours then offered a known number of P. dixoni eggs on a very small piece of fresh apple on a glass slide. Cockroaches were watched to ensure that apple+egg(s) were eaten, and slides were examined for unconsumed egg(s). Each was then given

abundant water and food (of one type only: rabbit pellet diet 94P, H. Archer and Son, Christchurch, New Zealand). Faecal pellets were removed daily to avoid reinfection and for examination in some cases). At the end of each experiment, cockroaches were dissected and their hind guts examined for nematodes.

Eggs used in infection experiments were obtained from i), females from cockroaches from the infected colonies; ii), females arising from some infection experiments; iii), faeces of infected cockroaches. The origin of eggs used in various experiments is indicated in Table 8. Female nematodes to be used as egg donors were kept individually in saline. The eggs they deposited, or eggs removed from them by dissection were used 4-120 days later. Eggs from host faeces were used 5 days after deposition. Faeces from experimentally infected cockroaches were examined microscopically for the presence of nematodes from the start of some experiments.

Twenty cockroaches from the infected colonies which had *P. dixoni* eggs in their faeces were isolated in individual containers and the numbers of nematode eggs passed daily over a 30 day period were determined. Their nematode burdens (infrapopulations) were then determined by dissection. A varying number of cockroaches (controls) from the naive colonies were treated identically during each experiment except that nematode eggs were not given.

RESULTS

i) *Protrellus dixoni* infrapopulation structure in field-collected and laboratory colony hosts

Adult cockroaches collected from Hexton and cockroaches from the infected colonies had 1-8 adult females (usually 1 - 3), 0-30 juvenile

Table 8. *Protrellus dixoni* infrapopulations resulting from feeding varying numbers/types of eggs to naive and infected *Drymaplaneta variegata*.

No. Ex., number of experiment. Orig. eggs, origin of eggs: A, "unknown" (unknown if female from which egg(s) taken were from infrapopulations which included an adult male); B, "fertilised" eggs (eggs from females from infrapopulations which included an adult male; C, total "fertilised" eggs from each B female remaining after single egg feeding experiments; D, autotokous eggs from female nematodes resulting from experiment 1; E, autotokous eggs from faeces of seven cockroaches each containing one adult female (resulting from Expt 2a); F, eggs as for E, fed back to seven cockroaches, each containing 1 female as a result of Expt. 2a ; G, adult female nematodes resulting from Expt. 2a (initially, each female was alone; subsequently, their parthenogenetically produced (= male) eggs were fed back to them; presumably each female had the capacity to mate with the added male); No. F: number of female nematodes from which eggs taken. No. E: number of eggs fed (all, entire female nematode fed to naive cockroach). CR No., number of cockroaches fed (all naive at the start of experiments except cockroaches in Expt. 4b). Cont.: number of control cockroaches for each experiment. Day Dis.: days after start of experiment cockroaches dissected. Total: % of cockroaches which became infected. Infra-population: Type, type of infra- population found on dissection; Type %, % of infected hosts with infrapopulation type.

No. Ex.	Orig. eggs	No. F	No. E	CR No.	Cont.	Day Dis.	Total	Infrapopulation Type	Total %
1a	A	10	1	88	14	60	64	1AF	47
								1AM	53
1b	A	10	2	36	7	60	72	1AM	46
								1AM + 1AF	15
								1AF or 1JF	15
								2AF	23
1c	A	30	30–50	42	12	60	100	1AM+1–8AF +0–10JF	64
								1AM+0–2AF +11–22JF	28
								JF +/– AF only	7
2a	B	7	1	88	19	60	41	1AM	81
								1AF*	19
2b	C	7	15–30	7		60	100	1AM	14
								1AF	14
								1AM+3,4AF	43
								1AM+28JF	14
								29JF	14
3a	D	4	1	23	5	40	61	1AM	100
3b	D	18	2–50	27	5	40	74	1AM	100
4a	E	7	2–6	28	5	30	57	1AM	100
4b	F	7	5–20	7	5	35	100	1AM+1AF	100
4c	G	7	all	7	3	70	100	1AM+0–6AF +0–20JF	100

* assumed by eggs in faeces, confirmed later by dissection
AM, adult male; AF, adult female; JF, juvenile female

females, but never more than 1 (sometimes no) adult male. Infection prevalence in 71 adult cockroaches collected at Hexton was 56% (58% of males, 52% of females) and in over half (55%) of these infected cockroaches, either 1:1, 1:2, or 1:3 adult male to adult female worm burdens occurred. In both male and female hosts, the mean adult male to female worm ratio was 1:2.2.

Newly hatched cockroaches, cockroaches from the naive colonies dissected periodically, and control cockroaches did not contain nematodes.

Cockroaches denied food and water for 24 hours immediately consumed the apple+egg(s) proffered, and all eggs were ingested. Eggs 4-120 days old were viable.

ii) Evidence for competition

Experiment 1, Table 8

The initial experiment, undertaken to determine if laboratory infection of cockroaches was possible, used eggs of "unknown" origin (i.e., no record was kept of the structure of the infrapopulation from which donor females came) from females in hosts from the infected colonies. When only 1 egg of "unknown" origin was fed to a series of naive cockroaches, approximately half of the resulting infections consisted of a single adult male and half a single adult female (Expt. 1a). No cockroach fed 2 eggs of "unknown" origin contained more than 1 adult male although a quarter of them had 2 adult females (experiment 1b). Similarly, when many such eggs (30-50) were given, no cockroach contained more than 1 adult male at the end of the experiment (1c) although some contained numerous adult (up to 8) and juvenile (up to 22) females (Appendix 4). In the latter experiment, all cockroaches without adult females had more than 10 juvenile females while most (79%) hosts

with adult female(s) had fewer than 5 juvenile females/host. Thus adult females were scarce if juvenile females were numerous and vice versa.

Experiment 2, Table 8

Seven females that came from mixed-sex (adult male present) infrapopulations provided eggs in this experiment. Three of these adult females were the only adult female present, but 4 came from infra-populations with 2 adult females. When single eggs from an individual female were fed 1 each to a series of naive cockroaches, the progeny of that individual donor female were either all male, all female, or both male and female, depending on which donor female was used (Expt. 2a). After these single egg infection experiments, some eggs (15 - 30) remained from each of the 7 donor females. These 7 groups of remainder eggs were fed en masse to 7 naive cockroaches (each receiving a group of eggs from a single female, Expt. 2b). Resulting infrapopulations included those with a single adult female, with a single adult male, with a male and adult or juvenile females, and with juvenile females only. Females from 2-adult-females/host infrapopulations did not produce progeny with a similar sex ratio. In one case, eggs from 1 female gave only a male when fed singly or en masse but eggs from the other female from the same host gave both male and female progeny. In the other case, eggs from 1 female gave only female progeny, while eggs from the other female from the same host gave both males and females. As in experiment 1, when many female nematodes were present at the end of the experiment, all were still juveniles; adult females usually occurred when only few females were present.

iii) Evidence for arrhenotoky

Experiment 3, Table 8

Eggs from female nematodes that resulted from single egg

infections (experiment 1a) resulted in 1 male only whether 1 (Exp. 3a) or many (Exp. 3b) eggs were fed to a series of naive cockroaches.

iv) Evidence for arrhenotoky and competition

Experiment 4, Table 8

Eggs collected from the faeces of cockroaches given 1 egg which resulted in a female (Expt. 2a, Table 8; Appendix 5) produced only lone males when fed to naive cockroaches (experiment 4a). Further such eggs collected from the same source and fed back to those sources (cockroaches in Expt. 2a containing lone unmated females) produced a male in each cockroach (experiment 4b). Each male was assumed to have had the capacity to mate with the female already present. When these presumably now fertilised females were fed entire one each to 7 naive cockroaches, resulting infrapopulations consisted of varying numbers of juvenile and adult females but only 1 adult male (experiment 4c). Again, maturity of females was inversely proportional to female numbers.

v) Evidence for intrasexual competition

Experiment 5, Cast Nematodes

Examination of faecal pellets produced by cockroaches given numerous eggs from lone, unmated females only (experiments 3b; 4a) showed that dead juvenile nematodes of indeterminate sex appeared from day 2 after the start of the experiment, dead juvenile males appeared from about day 9, and dead adult males from day 12. Adult males ceased to appear in the faeces after day 22.

Scans of faecal pellets produced by cockroaches given numerous eggs from females from mixed sex infrapopulations (experiments 1c; 2b; 4c) showed a similar pattern of dead male nematode appearance but dead juvenile females were identifiable by about day 14 and dead juvenile females of increasing size continued to appear in faeces up to about day

30. No adult females were passed. Eggs appeared on the faeces from day 50 onwards. When many juvenile females were found in a host, few had been found in faeces and vice versa. For example, 1 cockroach with an infrapopulation of 1 adult male and 2 adult females passed 21 dead nematodes (11 of indeterminate sex, 4 juvenile males, 6 juvenile females). Another cockroach with 1 adult male, 1 adult female and 28 juvenile females had passed only 4 juveniles of indeterminate sex.

vi) Evidence that crowding reduces per capita fecundity

Experiment 6

When few adult females were present in a host, per capita egg production was greater than when many were present (Fig. IV, F, 1; Appendix 6). Lone adult females producing fewer than 2 eggs/day were accompanied by 17 or more juvenile females, while those producing more than 3 eggs/day were accompanied by fewer than 6 juvenile females. Eggs were produced cyclically, with maximum egg appearance once every few days whether 1 or many adult females were present (Fig. IV, F, 1). Most of the eggs produced on a peak day were found on only 1 of the up to 10 host faecal pellets produced.

DISCUSSION

Evidence from field collected data showed that several thelastomatid species in several cockroach species undergo a selective reduction in infection intensity with host age which leads to regulation of the parasite population (Section IV, B, E). Similarly, field collected Drymaplaneta variegata never had more than one adult male and only few adult female Protrellus dixoni. The present study has shown that self-regulation of infrapopulations, suggested as the regulatory mechanism in other thelastomatids (Section IV B, E) probably occurs in P. dixoni.

Figure IV, F, 1

Fecundity and cyclical egg production in crowded and uncrowded Protrellus dixoni.

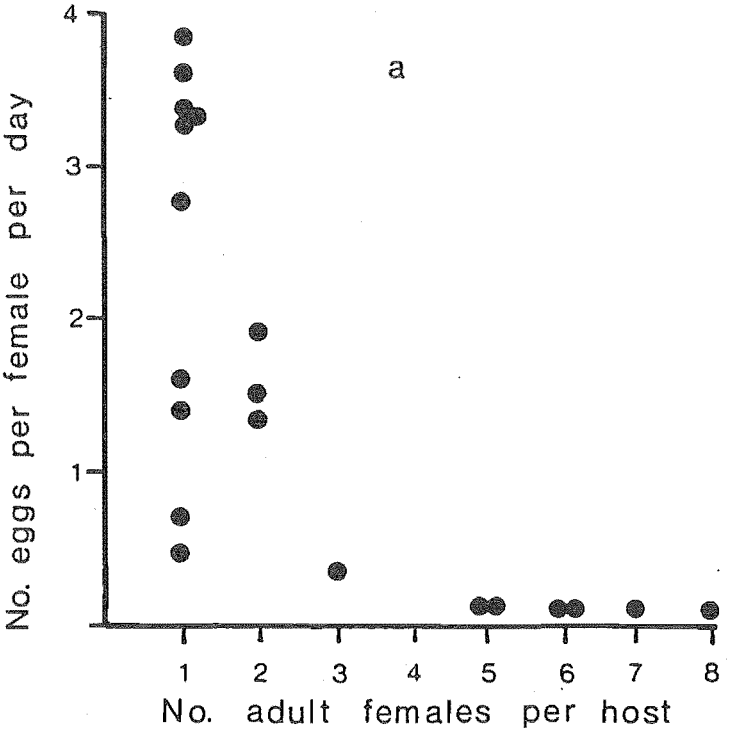
a) Fecundity

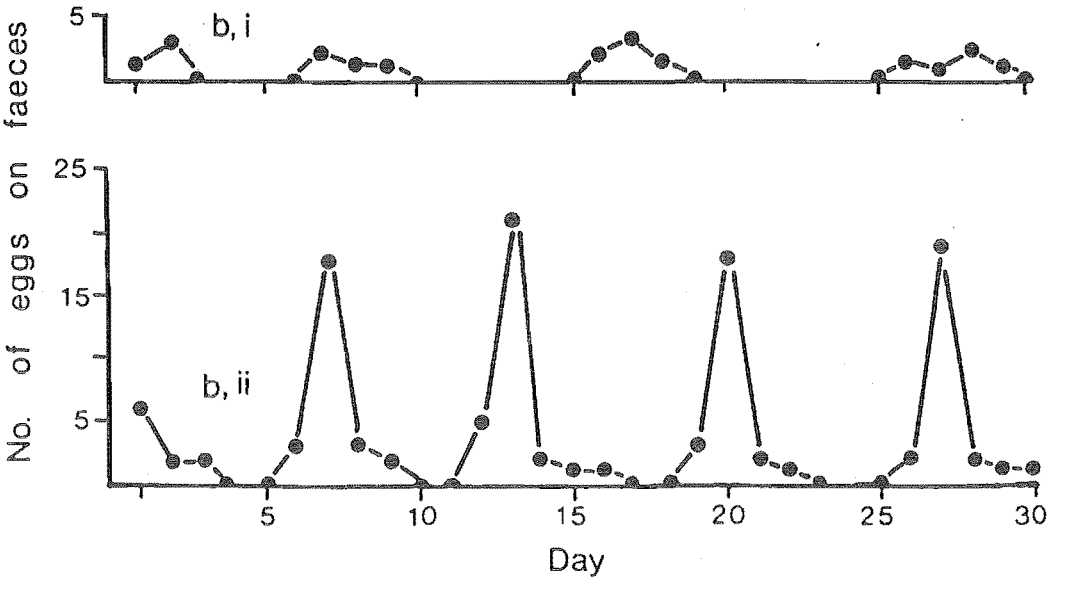
Single adult females producing <2 eggs/day are accompanied by 17-30 juvenile females; those producing >2 eggs/day accompanied by <7 juvenile females. Each point represents a single infrapopulation.

b) Cyclical egg production

i) host with eight adult female and two juvenile female nematodes.

ii) host with one adult female and no juvenile female nematodes.


a
No. eggs per female per day
4
3
2
1
1 2 3 4 5 6 7 8
No. adult females per host


b, i
b, ii
No. of eggs on faeces
5
25
15
5
5 10 15 20 25 30
Day

Reduction in Protrellus numbers/host/time is both density- and sex-dependent. Males apparently compete rapidly with males until, without exception, never more than one remains. The survival to adulthood of only one male is not due to the viability of only one egg, because when large numbers of male eggs (operational definition of "male eggs" - those that develop into a male) only or male and female eggs are fed to naive cockroaches, males of increasing maturity appear with time in the faeces. Evidence for a slower female-female competitive interaction can be inferred from the fact that juvenile females continue to appear in faeces after males have ceased to do so. Evidence for female-female interactions can also be inferred from the fact that when many females are present in an infrapopulation, none or few are adults. Reasons for the elimination of many juvenile females and the development to adulthood of the few remaining in one host, but not in another over the same time period, are unknown.

Mechanisms which may be responsible for regulation of thelastomatid infrapopulations were discussed in Section IV, B. Apart from regulation by environmental sex determination, these mechanisms were discounted. In P. dixoni, environmental sex determination (common amongst some groups of entomogenous nematodes occurring in the haemocoel, and amongst plant parasitic nematodes) can also be discounted on the grounds that single eggs given to naive cockroaches develop into either a male or a female, and that populations resulting from the simultaneous administration of eggs of mixed sex result in mixed sex infrapopulations. It is probable therefore, that regulation occurs through male-male and female-female parasite-mediated chemical interference competition. The nematodes themselves may produce some kind of sex-specific anthelmintic. This can be inferred from the fact that single sex infrapopulations are regulated, and males are eliminated (except one) before females, which

continue to compete. Rapid elimination of males compared to females may be related to their shorter maturation time. Many different thelastomatid species have infrapopulations which are apparently regulated (Section IV B, E), and regulation may be parasite-mediated in these cases.

In P. dixoni, as in B. monandros (Section IV, C), fecundity and crowding are inversely related. Thus competitive reduction in infection intensity benefits both the male and the one-few females that survive because it increases their chances of reproductive success. In addition, P. dixoni produces eggs cyclically and in batches as do other thelastomatids (Section IV, C). Clumping of eggs in the environment is likely to lead to enhanced reproductive success for the parent nematode because a naive cockroach is likely to acquire a male and female nematode that are siblings.

Transmission success in this and other thelastomatids may be enhanced if cockroaches are attracted to and eat cockroach faecal pellets. Other cockroaches require an intake of faecal material produced by their own species for normal growth (Bell, Parsons & Martinko, 1972; Burk & Bell, 1973; Chauvin, 1946, 1967; Izutsu, Ueda & Ishii, 1970). Such faecal material contains a growth accelerant and chemical attractant which is species specific (Bell, Burk & Sams, 1973; Chauvin, 1967; Ishii & Kuwahara, 1967, 1968; Metzger & Trier, 1975; Roth & Cohen, 1973; Sommer, 1975).

Unmated P. dixoni females produce eggs that develop into males only. Only females that have access to a mate produce female offspring. This suggests that females are the product of amphimixis and thus diploid, while males are the product of arrhenotokous parthenogenesis

(the production of haploid males from unfertilised eggs) and thus haploid. There is no evidence that deuterotoky (the parthenogenetic development of both males and females from unfertilised eggs) occurs. Deuterotoky has not been found amongst nematodes (Bell, 1982; Poinar & Hansen, 1983) and is considered a rare and aberrant process (Bell, 1982).

Females with access to a mate may produce either all male or all female or both male and female progeny. In one case, one female of a pair from an infrapopulation containing a male produced only males, while the other produced both males and females. There may be several explanations for the production of male eggs by females in mixed-sex infrapopulations. Firstly, such females may avoid insemination or have the capacity to withold fertilisation from some of their eggs; thus they may have the capacity to control the sex ratio of eggs as do most haplodiploids (Borgia, 1980). Conversely, some males may be sterile or may not have enough sperm to fertilise some/all eggs. Alternatively, males may develop after pseudogamy (use of male sperm to initiate development but no incorporation of paternal genetic information) or males may develop from diploid eggs if the alleles on the sex locus are homozygous.

Some other female nematodes, such as the insect parasites Fergusobia curriei and Heterotylenchus autumnalis, produce male progeny parthenogenetically (Fisher & Nickle, 1968; Nickle, 1974). More recently, Adamson (1981a, 1983, 1984) and Adamson & Petter (1983a,b) reported haplodiploidy and arrhenotoky in fourteen nematode species parasitic in cockroaches, amphibians, reptiles, and mammals, and concluded (Adamson, 1984) that several other species were haplodiploids. Apart from F. curriei and H. autumnalis, these nematodes, like Protrellus, are oxyuroids. Together, they represent the four oxyuroid

families (Oxyuridae, Thelastomatidae, Pharyngodonidae, Heteroxynematidae). Haplodiploidy and arrhenotokous parthenogenesis is thus widespread amongst the oxyuroids of vertebrates and probably of invertebrates.

Haplodiploid systems are usually associated with spanandry, i.e., population sex ratios skewed towards females (Adamson, 1983; Hamilton, 1967). It is surprising, therefore, to find that P. dixoni eggs of "unknown" origin, (which can be considered as eggs taken at random from the entire parent suprapopulation), give a 50:50 sex ratio if fed one each to naive hosts. However, in D. variegata given numerous eggs of mixed sex, spanandry results because of the selective reduction in infection intensity. Spanandry is also seen in infrapopulations in naturally infected, wild-collected hosts.

SECTION V

DISCUSSION

SECTION V

DISCUSSION

A) INTRODUCTION

The aim of this thesis was to investigate the regulation of thelastomatid populations in cockroaches and to determine what form this regulation takes. Empirical data from both field and laboratory studies were gathered. The major findings of this research were that population regulation does occur, that this regulation is Bradley (1972, 1974) Type 3 in nature, and that regulation is probably mediated through the production of some sex-specific anthelmintic by the nematodes themselves.

All observations of thelastomatid populations in field collected hosts and populations manipulated in the laboratory provided evidence that regulation occurs. In spite of their small size compared to females, no host had more than one adult male. Juvenile males were rare and infrapopulations with two juvenile males were very rare. Juvenile females were relatively numerous but the number of adult females per host was small. A monogamous infrapopulation was the modal type in four out of seven thelastomatid species and monogamy was common amongst the remainder. From the little data available in the literature on thelastomatid population structure, it is concluded that regulation is common amongst this family of nematodes in cockroaches and other arthropods.

It is clear that in all species (except perhaps Protrellus dalei in Celatoblatta peninsularis), there is a redundancy of transmission above that required for mere persistence of the parasite. Thus the first prediction of Bradley's (1972, 1974) hypothesis is satisfied. Infection prevalence was high in hosts collected in the

field. In one cockroach (Parellipsidion pachycercum), infection prevalence and intensity (of Blatticola monandros) was high in small nymphs, but while prevalence increased with host age, intensity decreased. In another cockroach (Celatoblatta vulgaris), infection prevalence (of Protrellus dalei) was low in small nymphs. However, while prevalence increased in larger cockroaches, intensity decreased. From these facts it can be assumed that the number of eggs ingested is greater than the number of nematodes that survive to maturity.

Because there is redundancy of transmission, stabilising mechanisms must exist in order that populations do not increase exponentially. As outlined in the introduction, Bradley (1972, 1974) proposed three types of way in which the upper limits of parasite numbers might be determined. These include Type 1 regulation, where parasite numbers are determined by changes in transmission; Type 2 regulation, where numbers are determined by a host sterile immune response or by differential death of overburdened hosts; and Type 3 regulation, where numbers are determined by premunition, immunity, or similar factors.

B) THELASTOMATID POPULATIONS AND BRADLEY'S THREE TYPES OF POPULATION REGULATION

Amongst cockroach thelastomatids, there is no evidence that long term determination of population size is achieved by changes in transmission (Type 1 regulation). Bradley (1972, 1974) predicted that populations determined by changes in transmission would be unstable because negative feedback is not involved. Evidence from temporal changes in B. monandros (Section IV, D) support this hypothesis. In this case, infection incidence, intensity, and infrapopulation structure were adversely affected by unseasonable weather, but only temporarily.

The population returned to its previous state after perturbation-caused instability. Esch (1982) considered that any parasite population affected by unpredictable density-independent abiotic factors (such as unseasonable aridity) must possess physiological or behavioural cushions to withstand such stress. Obviously, this is the case in B. monandros. In all species, the upper limit of infection intensity was apparently not affected by any increase in transmission. In Drymaplaneta variegata, the number of adult Protrellus dixoni in mature infrapopulations was low in spite of high transmission rates. Thus thelastomatids resemble the majority of parasites in which determination of population size by Type 1 factors is rare (but for examples of parasites which are determined by such factors, see Awachie, 1966; Kennedy, 1974).

There is no evidence that cockroach thelastomatid populations are limited by Type 2 regulation. Arthropod defense mechanisms against gut parasites are probably non-existent (Lackie, 1980). Thus sterile immunity does not occur in these hosts. Nor, apparently, is there differential death of overburdened hosts.

Regulation, then, occurs at the level of the host individual (Type 3 regulation). Regulation of number of worms can not be attributed to host defensive responses (there is no premunition or partial immunity), to physical interference between the parasites, or to parasite competition for some limiting factor. It is also probable that distribution patterns are not the result of skewed egg sex ratios. If only few male eggs are produced, sex ratios of established infra-populations may be skewed towards females. However, the occurrence without exception of only one adult male in a host (with or without females) can not be due to a scarcity of male eggs in the environment

and the subsequent ingestion of only one of these. Rather, monandry is the result of mechanisms occurring after ingestion of eggs. One such mechanism is environmental sex determination. This mechanism can be discounted as a cause of monandry in thelastomatids.

C) THELASTOMATID SELF REGULATION

Thus it seems likely that the cause of regulation in these parasites is one omitted by Bradley. It is the nematodes themselves which regulate their own infrapopulations, probably through chemical interference competition. Although self-regulation is not one of the "classical" types of Bradley's Type 3 regulation, it is efficient because it is density- and sex-dependent and operates with increased severity when population sizes are large, thus stabilising the population.

Self-regulation by thelastomatids may have evolved because arthropods apparently lack defense mechanisms against gut parasites. For a parasite to merely gain entry and remain unmolested by an immune response is not sufficient for a long-term, well-balanced host-parasite system (Lackie, 1980). The mere persistence of a parasite in a host does not necessarily indicate stability (Kennedy, 1977). Thus, for parasites which live in hosts with limited immunological competence, it may be beneficial for individuals in infrapopulations to stabilise the number in that infrapopulation by interference competition because, if this did not occur, numbers might increase to the point where the host and hence the parasite is harmed. Furthermore, if individual fitness is directly proportional to reproductive rate, those thelastomatids which survive to adulthood in reduced infrapopulations have increased fitness.

D) PREVALENCE OF THE "CROWDING EFFECT" AMONGST PARASITES

Competition and elimination of supernumerary parasites, and reduced fecundity or adult size when parasites are overcrowded are manifestations of the "crowding effect" (Kennedy, 1975). The crowding effect is common in helminths (Kennedy, 1977). Amongst many nematode groups, infection intensity is often about the same in spite of numbers initially ingested (Ackert, Graham, Nolf & Porter, 1931; Dobson, 1974; Donald & Waller, 1982; Harkema, 1936; Jarrett, Jarrett & Urquhart, 1968; Kassai, 1982; Kendall & Harding, 1970; Tinsley, pers. comm.; Yong & Dobson, 1982, 1983). Often, crowding of nematodes affects establishment (Mykytowycz & Dudzinski, 1965), sex ratio (Christie, 1929; Comas, 1927; Couturier, 1963; Parenti, 1965; Tingley, 1982; Vandel, 1932), adult size or rate of development (Couturier, 1963; Dunsmore 1960; Upton et al., 1983; Welch, 1959, 1963; Yong & Dobson, 1983) or per capita fecundity (Andrews, 1936; Kort, 1962; Krupp, 1961; Sarles, 1929). Amongst nematodes of sheep and other economically important mammals, presence of adult worms is thought to induce arrest of juveniles, while removal of adults allows larval development to proceed (Charleston, 1982; Dunsmore, 1963; Gibson, 1953; Roberts & Keith, 1959).

Nearly all cestodes exhibit an intraspecific crowding effect in their definitive host (Kennedy, 1975). These effects are manifested in several ways. In some, the size of adult worms is inversely related to population density (Andersen, 1972; Hunninen, 1935; Litchford, 1963; Read, 1959; Read & Simmons, 1963; Roberts & Mong, 1968; Shorb, 1933; Wardle & Green, 1941; Woodland, 1924). In others, crowding delays strobilation and so-called primary strobila develop (Halvorsen & Anderson, 1974; Hunninen, 1935), or per capita fecundity is reduced (Ghazal & Avery, 1974; Jones & Tan, 1971; Weinmann, 1958). Often,

numbers of worms that finally establish are similar regardless of how many are ingested (Boddington & Mettrick, 1981; Coil, 1963; Halvorsen & Williams, 1968; Self & Pipkin, 1966; Williams & Halvorsen, 1971).

Intraspecific crowding effects have also been noted in parasitic arthropods (Mock, 1974; Simmonds, 1943), protozoans (Long, 1967; Williams, 1973), trematodes (Anderson, Whitfield, & Mills, 1977; Basch, 1969; Boray, 1969; Fried & Nelson, 1978; Mills, Anderson & Whitfield, 1979; Nollen, 1983; Tandon, 1973; Vermund, Bradley & Ruiz-Tiben, 1983; Willey, 1941), and acanthocephalans (Awachie, 1966; Burlingame & Chandler, 1941; Chubb, 1964; Crompton, Keymer & Arnold, 1984; Graff & Allen, 1963; Hine & Kennedy, 1974; Holmes et al., 1977; Uznanski & Nickol, 1982).

E) THE CAUSAL MECHANISMS OF THE CROWDING EFFECT

i) Introduction

The immune responses of the host, or competition for limiting resources are often invoked to explain the crowding effect. However, the crowding effect is quite distinct in its causal mechanisms, though not in its manifestations, from host mediated immune responses (Kennedy, 1975). In many cases where hosts are known to be immunologically competent, immunity can not fully account for observed parasite distribution patterns (Crompton et al., 1984; Holmes et al., 1977; Keeling, 1961; Krupp, 1961 Mykytowycz & Dudzinski, 1965; Nickol, 1977; Reinecke, Bruckner & De Villiers, 1980; Schad, 1977; Singhvi & Johnson, 1976, 1977). However, the identification of regulatory mechanisms has been elusive (Hirsch, 1977; Hunter, Weinmann & Hoffman, 1961; Kennedy, 1982; Keymer, 1982; Pence & Windberg, 1984). It could be that in these cases, self-regulation by competitive exclusion plays some part in

generating patterns of distribution. Self-regulation may play a role in the regulation of gastro-intestinal nematodes of sheep (I. A. Barger, CSIRO, Armidale, Australia, pers. comm.) and may be widespread amongst parasites of vertebrates (R. C. Tinsley, Queen Mary College, University of London, pers. comm.).

ii) Pheromone production

Thelastomatids may regulate their own infrapopulations by producing a sex specific anthelmintic pheromone. Substances produced by one member of a species which inhibit establishment, growth or fecundity of conspecifics are found in a variety of organisms (for example, plants (Muller, Muller & Haines, 1964; Rice, 1974); slime moulds (Loomis, 1975); cnidarians (Davis, 1967; Schaller, 1976); bacteria, protozoa, planarians, molluscs, ostracods, crustaceans, echinoderms, insects, fish, and amphibians (Rose, 1960, 1965)). An expanding literature suggests that many aspects of helminth physiology and behaviour are also mediated by chemical messages or pheromones (Bone, 1982; Imperia, Fried & Eveland, 1980).

That the anthelmintic hypothesised for thelastomatids is sex specific can be inferred from the efficacy of population regulation in single sex infrapopulations and the rapid elimination of all males (except one) before that of females in mixed sex infrapopulations. Competition amongst females continues after supernumerary males are lost, and supernumerary females continue to be eliminated.

Although pheromones have been studied in at least 24 nematode species, little is known of their activity. Some have been shown to have a negative effect. Crowding of male Nippostrongylus brasiliensis (Travassos, 1914) Travassos & Darriba, 1928 in mice prior to their

exposure to female pheromone gradients diminishes male responses to the pheromone because males interfere chemically in some way with each other's ability to respond (Bone, Shorey & Gaston, 1977). Bone & Shorey (1977) suggested that interference is due to the release of an inhibitory pheromone by some males. Meerovitch (1965) showed that substances with juvenile hormone (= JH) activity interfere with development in nematodes and substances similar to JH have since been found in a number of nematodes (Davey, 1977; Hitcho & Thorson, 1971; Rogers, 1973). When nematodes are cultured in media containing JH, moulting fluid may be prematurely released, juvenile development may be arrested, and moulting and formation of male copulatory appendages may be inhibited (Boisvenue, Emmick & Galloway, 1977; Davey, 1971; Johnson & Viglierchio, 1970; Shanta & Meerovitch, 1970). Schad (1977) suggested that nematodes of sheep and other economically important animals recognize their own density through some pheromone-like substance which in turn influences the numbers arresting and developing. Reinecke et al. (1980) found sheep initially given large doses of Trichostrongylus axei were resistant to Haemonchus contortus given subsequently. They (Reinecke et al., 1980) found no evidence that this was due to an immune reaction and suggested that T. axei make abomasal fluid unsuitable for H. contortus.

Most work on parasite pheromones has been conducted amongst cestodes. Halvorsen & Williams (1968) suggested a conditioning of the habitat by secretions or pheromones from crowded cestodes was common and that this influenced the development and behaviour of other individuals in a population. The hypothesis that Hymenolepis diminuta (Rudolphi, 1819) Blanchard, 1891, releases a substance which inhibits the growth of other worms (Roberts, 1961) has been tested by Roberts and his co-workers. H. diminuta incubated in vitro from crowded infections showed a decreased rate of DNA, RNA, and protein synthesis (Bolla &

Roberts, 1971). Insler & Roberts, (1980a) prepared a "worm conditioned saline" (WCS) by incubating crowded worms in saline, then tested the incorporation of ^{3}H-thymidine into DNA of uncrowded worms incubated in WCS compared to worms incubated in normal saline. They (Roberts & Insler, 1982) concluded that these cestodes do secrete some growth inhibiting "crowding factor". Of the many compounds identified in WCS, cyclical nucleotides, acetate, D-glucosaminic acid, and succinate have all been found to inhibit ^{3}H-thymidine incorporation into DNA (Insler & Roberts, 1980b; Zavras & Roberts, 1984, 1985). Though the mechanism of action of these compounds is unclear, they may work through an alteration of the cellular cAMP/cGMP ratio (Zavras & Roberts, 1985). Inhibitory substances with similar activity may be produced by thelastomatid nematodes in cockroaches.

F) THE PREVALENCE OF UNDERDISPERSED PARASITE DISTRIBUTION PATTERNS

Thelastomatid population self-regulation leads to a more-or-less underdispersed (regular) distribution pattern when infrapopulations comprised of adult nematodes only are considered. Underdispersion is considered to be very rare amongst parasites, most of which have an overdispersed (aggregated) distribution pattern (Anderson, 1982a; Anderson & May, 1978; Crofton, 1971; Crompton et al., 1984). Thus most hosts tend to harbour few parasites while a few hosts harbour the major portion of the parasite suprapopulation (Anderson & Gordon, 1982). Only a few cases of Poisson (random) distributions in parasites have been reported (eg, Hopkins, 1959; Kennedy & Burrough, 1981). While overdispersion is certainly common, it can not yet be concluded that underdispersion is rare. Generalisations concerning parasite distribution patterns have been based on observations of parasites in vertebrate

hosts. Vertebrate parasites are intensively studied because of their medical and economic importance, yet most host-parasite interactions must occur in invertebrate hosts. Hence underdispersion, particularly amongst invertebrate gut parasites, may be more common than expected or predicted by models constructed by theoretical workers to explain parasite distributions. A model designed to describe the dynamics of underdispersed parasites (Anderson & May, 1978) showed that such systems would be ineluctably unstable. This is not true in reality. Esch et al. (1977) predicted that underdispersed parasite populations, while rare, might arise if competition for resources is severe or if chemical substances are produced that prevent other organisms from becoming established nearby. This prediction is probably correct.

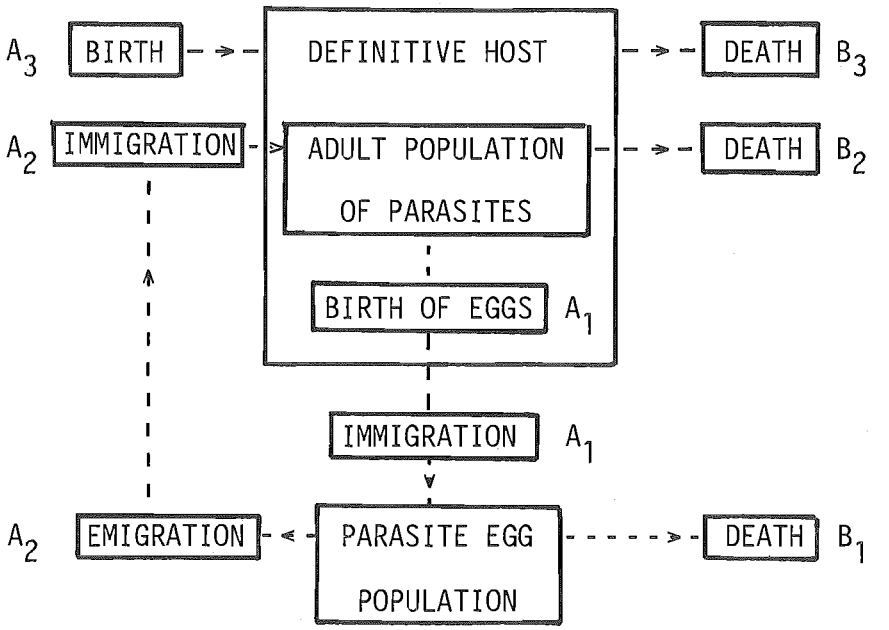
G) A SIMPLE MODEL DESCRIBING THELASTOMATID POPULATION REGULATION

Some models are useful because they summarise information about systems and stimulate ideas for further research. A simple, deterministic model describing the interaction between a direct life cycle helminth parasite in a single host species is that of Anderson, 1976. This model is given in a modified form below. The cycle involves three distinct populations (the host, adult parasites, and eggs). If immigration and emigration of the host population (likely to be small, say, in Parellipsidion pachycercum at Kaituna Valley) are ignored, the flow of parasites through the cycle is controlled by 6 rate parameters

A_1 = egg production rate	B_1 = egg death rate
A_2 = host infection rate	B_2 = parasite death rate
A_3 = host birth rate	B_3 = host death rate

Parasite death rate (B_2) has three components (May & Anderson, 1978): 1, loss due to natural host mortality; 2, parasite induced host

death; and 3, parasite death generated by natural parasite mortality within the host due to, for example, parasite senescence. While 1 and 3 must operate in thelastomatids, 2 does not. The system can be represented diagrammatically thus



Assuming that, as in thelastomatids, the parasites do not affect host survival, the basic features of the adult parasite population P_t within the host, and the egg population W_t in the external habitat are represented by the following equations

$$\frac{dW_t}{dt} = A_1P_t - B_1W_t - A_2W_t$$

$$\frac{dP_t}{dt} = A_2W_t - B_2P_t$$

where the instantaneous rates are assumed for simplicity to be constant.

It is assumed in this model that the rate of infection of the host is directly proportional to the density of the infective stages. In this case, both egg and adult populations either grow or decay exponentially depending on the parameter values and thus no equilibrium state is achieved. To achieve an equilibrium between host and parasite, some form of density-dependent regulatory process must operate on the dynamics of the interaction. If any one of the parameters that determine the flow of parasites through the cycle is density-dependent, then regulation will occur. Thus if B_2 is density-dependent, the population is regulated according to

$$P = \left[a \frac{B_2}{A_2} (B_1 + A_2) \right]^{\frac{1}{b}}$$

where a represents the maximum number of nematodes/host and b determines the severity of the density-dependent responses (Anderson, 1976). In thelastomatids, B_2 is density-dependent. Therefore, regulation occurs. Another density-dependent phenomenon amongst thelastomatids is reduced egg production when females are crowded, but what effect this has on population dynamics is unknown.

H) THELASTOMATIDS AND FECUNDITY

Parasitologists generally view high fecundity as an adaptation for the parasitic mode of life (Cole, 1954; Esch et al., 1977), although some (Jennings & Calow, 1975) conclude that high fecundity is a direct and automatic consequence of the nutrient rich environment provided by the host. Anderson (1976) thought that parasite egg production rate (A_1) will always be many orders of magnitude greater than host birth

rate. Over a 30 day period, egg production by the cockroach Drymaplaneta variegata is about 97-160 (in 7-10 oothecae, Section II, E) while maximum egg production by its parasite (Protrellus dixoni) in adult hosts was 117 (Appendix 6). In Parellipsidion pachycercum, oothecae contain 12-14 eggs each (Section II, B) but the interval between oothecal depositions is unknown. However, it is unlikely to be shorter than that of D. variegata or other cockroaches (interval between oothecal deposition in others = 3-22 days, Guthrie & Tindall, 1968). Maximum egg production by Blatticola monandros in adult P. pachycercum was 160 over a 30 day period (Table 6). Assuming all cockroach and nematode offspring are viable, fecundity of thelastomatids in adult cockroaches is apparently not many orders of magnitude greater than host birth rate.

Nevertheless, infection prevalence is high in these cockroaches. Several factors may account for this. Firstly, adult female nematodes in juvenile cockroaches may contribute significantly to the pool of eggs in the environment in spite of their smaller size and fewer eggs. Secondly, thelastomatid eggs may be viable and thus available to newly emerged cockroaches for long periods if environmental conditions are suitable. Eggs of some species may be very resistant. For example, the host of Blatticola barryi (Celatoblatta quinquemaculata) lives above the tussock line in the alpine zone of some Otago ranges (Johns, 1966). In this environment, B. barryi eggs probably experience extremes of temperature and fluctuations in humidity. Eggs of thelastomatids parasitic in coleopterans, dipterans and lepidopterans can remain viable for at least three months (Dale, 1970) and eggs of the cockroach thelastomatid Hammerschmidtiella diesingi are viable for at least 60 days (Dobrovolny & Ackert, 1934). P. dixoni eggs are viable

for at least 120 days (Section IV, F). Thus the pool of infective-stage thelastomatid eggs in the environment may be large. Thirdly, transmission may be enhanced if cockroaches are attracted to and eat cockroach faecal pellets (Section IV, F). Finally, once established, thelastomatids may persist in cockroaches for a long time (they survive host moults).

I) THELASTOMATIDS AND r- AND K-SELECTION

A discussion of parasite population regulation can be framed in terms of Dobzhansky's (1950) concept of r- and K-selection (Cohen, 1983; Esch et al., 1977; Seidenberg, Kelly, Lubin & Buffington, 1974). The set of correlates created by Pianka (1970) for the purpose of comparing and contrasting r- and K-strategists and discussed by Esch et al. (1977) in relation to parasites can be considered in the light of what is known about thelastomatid strategies. The considerable discussion amongst ecologists in recent years for and against the concept (for example, see Stearns, 1984) is avoided in this discussion. Pianka's (1970) correlates are based on the following:

1) Climate: r-selection - variable and/or unpredictable; uncertain.

K-selection - fairly constant and/or predictable; more certain.

Thelastomatids are sometimes subject to selection forces which are characteristic of r-strategists. In this they resemble other parasites (Esch et al., 1977). They are affected by climatic variability acting directly on the egg stage, or indirectly when such variability adversely affects the host (Section IV, D).

2) Mortality: r-selection - often catastrophic, non-directed density-independent.

K-selection - more directed, density-dependent.

Thelastomatids are primarily subject to selection forces which are characteristic of K-strategists because mortality is density dependent and directed.

3) Survivorship: r-selection - high initial mortality with gradual decline and subsequent lower mortality among older individuals.
K-selection - either a, relatively low mortality in early age classes with subsequent mortality continuing to remain low until near the limit of longevity; or b, mortality rates proceeding at the same rate regardless of age.

Thelastomatids are subject to selection forces which are characteristic of r-strategists because initial mortality is high. In this they resemble other parasites (Esch et al., 1977).

4) Population size: r-selection - variable in time, non equilibrium, usually well below the carrying capacity of the environment, unsaturated communities or portions thereof, ecological vacuums, recolonization each year.
K-selection - fairly constant in time, at or near carrying capacity of the environment, saturated communities, no colonisation necessary.

Thelastomatids are subject to selective forces which are characteristic of K-strategists because population size (ie, infrapopulation size) is fairly constant in time and near the carrying capacity of the environment, and no recolonisation (ie, seasonal colonisation) occurs. Most other parasites are r-strategists (Esch et al., 1977).

5) Intra- and interspecific competition: r-selection - variable, often lax.
K-selection - usually keen.

Thelastomatids are obviously K-strategists. Intra- and interspecific

competition is also common amongst other parasites.

6) Longevity: r-selection - short, usually less than one year.

K-selection - longer, usually more than one year.

The longevity of adult thelastomatids is unknown, but it is likely to be at least several months. Amongst other parasites, life spans range from a few hours in protozoa to five years in some trematodes (Esch et al., 1977).

7) Relative abundance: r-selection - often does not fit MacArthur's broken stick model (intrinsically uniform division of some major environmental resource).

K-selection - frequently fits MacArthur's model.

Thelastomatids are subject to selective forces which are characteristic of K-strategists because they are underdispersed; most other parasites are overdispersed.

8) Selection favours: r-strategists - rapid development, early reproduction, semelparity (single reproduction), small body size, high r_{max} (maximum energy to intrinsic rate of natural increase).

K-strategists - slower development, greater competitive ability, delayed reproduction, iteroparity (repeated reproductions), larger body size, lower resource threshold (energy to maintainance and the production of a few extremely fit offspring).

Thelastomatids are apparently not very fecund compared to other nematodes with similar generation times (an important consideration when estimating biotic potential; Crofton, 1966; Pianka, 1970). In these nematodes, generation time (the period between egg ingestion and the maturation of an egg producing female) was 50 days in Protrellus dixoni; 30 days in Haemonchus contortus (Crofton, 1966); 50-80 days in Ascaris

lumbricoides and 40-50 days in Necator americanus (Anderson, 1982d). Longevity of adult female P. dixoni is likely to be at least several months; of H. contortus, several weeks (Schad, 1977); of A. lumbricoides, 1-2 years, and N. americanus, 3-4 years (Anderson, 1982d; Crofton, 1966). The maximum eggs/female/day in P. dixoni= 3.83 (Appendix 6); in H. contortus= 10,000 (Kennedy, 1975); in A. lumbricoides= 200,000 and N. americanus= 5,000-10,000 (Cheng, 1973, pp. 32, 633). Therefore, if a female P. dixoni produced the maximum number of eggs/day for two years, the total number of eggs produced over that time would be less than half that produced on any one day by any of the other nematodes considered above. Thus thelastomatids resemble K-strategists because they have a low r_{max} (compared to other parasites). They also resemble K-strategists because they are competitive and iteroparous, and probably survive in their host for a substantial part of the host's life.

In summary, thelastomatids have certain features that are typical of r-strategists, but even more which are typical of K-strategists. Jennings & Calow (1975) suggested that parasites, particularly endoparasites, follow both an r- and K-strategy, and that this is only possible because of the stable, nutrient rich environment. In contrast, Esch et al. (1977) argued that most parasites are r-selected.

J) THELASTOMATIDS AND INBREEDING

i) Clumping of eggs and inbreeding

The majority of parasites have an overdispersed distribution pattern. A major determinant of overdispersion is the spatial clumping of infective stages (Anderson, 1982, b; Crofton, 1971; Keymer, 1982; Keymer & Anderson, 1979). However, amongst thelastomatids of cockroaches, clumping of infective stages does not affect dispersion although it must

have some effect on population genetics. Thelastomatid females in monogamous infrapopulations have the capacity to produce both male and female eggs. Since monogamous infrapopulations are common, many of the batches of eggs in the environment will be composed of siblings of both sexes. When such a sibling batch of eggs is ingested by a naive cockroach, the nematodes that survive to adulthood will be very closely related, as will their progeny. Even when batches of eggs produced from mixed-sex infrapopulations with more than one adult female are considered, female progeny of all the mothers present will be related because they will have the same father. In addition, some of these females will share half their genome with their brother and future mate. Batch egg production is not unique to those thelastomatids investigated in this study. Many other species produce clumps of eggs and these are often "glued" together, attached by filaments, or eggs contain two embryos (Section IV, C). Therefore, there must be inbreeding in thelastomatid populations.

ii) Advantages and disadvantages of inbreeding

Inbreeding is generally considered to be detrimental (van den Berghe, 1980; Maynard Smith, 1978; Rogers & Ulmer, 1962) because 1), deleterious genes are more likely to be fully expressed; 2), beneficial interactions (heterozygous advantage or over-dominance) between different alleles at the same genetic locus are lost; 3), offspring are insufficiently variable for one or other of them to cope with a varying environment and 4), offspring are more like each other and so compete more intensely (Bateson, 1983). However, Shields (1982a, b, 1983) and Bateson (1983) have pointed out that there may be disadvantages to outbreeding. Some of these disadvantages include 1), meiotic loss; 2), those genes required for adaptation to a particular environment are

lost or suppressed; 3), co-adapted gene complexes are broken up by recombination (recombinational load) and 4), the parental genes are less well represented in the next generation. By the same token, advantages to inbreeding include the preservation of complexes of interacting alleles at different loci that have been coadapted by a common selective history, and the enhancement of individual fitness because parental genomes are transmitted as faithfully as possible, thus reducing meiotic loss (Borgia, 1980; Bull, 1979; Moore & Ali, 1984; Shields, 1982a, b, 1983).

Meiotic loss is a product of "sharing" offspring. For a female, outbreeding yields a 50% share of the genome for each zygote produced. This represents a two-fold loss when compared to the 100% share available to females reproducing the same number of zygotes by asexual parthenogenesis (Shields, 1982a). In an outbreeding system, once an integrated, coadapted combination of alleles, at many interacting loci, is produced by an incident of parental recombination and gametic fusion, it is not transmissible to subsequent generations, being broken apart by subsequent recombinational events. The greater the genetic difference between mates, the greater the recombinational load, as more and more alleles with different selective histories are thrust together into a single novel genome (Thompson, 1976).

Although exclusive parthenogenesis does prevent meiotic loss and does permit exact transmission of parental genomes, preventing recombinational load, it too is unable to transmit precise duplicates of successful parental genomes. If a mutation occurs in an asexual organism, the continued presence of that mutation (barring back-mutation) is assured in all its descendents. In contrast, inbreeding sexuality favours copying fidelity of a successful ancestral genome in the face of

mutation and disadvantageous alleles are expressed and eliminated in waste gametes (Borgia, 1980; Shields, 1982a, b, 1983).

iii) Haplodiploidy, inbreeding, and scarcity of males.

In thelastomatids, males are probably haploid. All genes act like dominants and there is no suppression of deleterious recessive alleles by normal dominants. Since the sperm cells are identical in genotype to the male that produces them, beneficial genes are likely to be spread more rapidly in haplodiploid than diplodiploid systems, whereas disadvantageous genes should not be able to accumulate (Bruckner, 1978). Heterotic mechanisms (the superior performance of heterozygotes relative to homozygotes) are effective only in the diploid part of the population and are thus not as important as in diplodiploid systems (Bruckner, 1978; Hartl, 1971). Inbreeding depression in diplodiploid species is caused by the appearance of "hidden" deleterious alleles and by the breakdown of heterotic mechanisms. Thus haplodiploid systems should be less affected by inbreeding, the haploid part of the population experiencing conditions that are similar to the homozygous condition of individuals from inbred diplodiploid species (Bruckner, 1978).

Arrhenotoky has received less attention in the literature than thelytoky in spite of the fact that it may occur in as many as one-quarter of all arthropod species, some rotifers (Borgia, 1980) and probably all oxyuroid nematodes (Adamson, 1983, 1984). Haplodiploidy is thought to have arisen from diplodiploid systems, and it has been suggested that in haplodiploids, inbreeding reduces many of the costs associated with the difficulties encountered during transition to haplodiploidy (Borgia, 1980; Brown, 1964; Hartl & Brown, 1970). Thus inbreeding and haplodiploidy are often found together (Borgia, 1980;

Ghiselin, 1975; Hamilton, 1967; Trivers & Hare, 1976). It is interesting to note that in haplodiploid systems, males transmit only maternally derived genetic information (Borgia, 1980; White, 1973). The selective advantage for the evolution of male haploidy stems from a two-fold representation of maternal genes in gametes of haploid sons in comparison to diploid sons (Bull, 1979). Only mated females are able to produce female offspring but this places no more of a premium on mating than in diplodiploid systems.

Hamilton (1967) has observed that among small arrhenotokous arthropods, whenever reproduction is regularly by sibling mating, there seems to be extreme economy in the production of males. For example, amongst 26 species of sib-mating arrhenotokous mites and insects parasitic on plants and other insects, over half have only one or two males, but up to fifty females per host. Hamilton (1967) thought that these sex ratios were determined by the parent insect or mite, although Hartl (1971) has pointed out they could be due to other causes, including competition between males. He (Hartl, 1971) thought that in such systems, males should be rare because a female's best strategy is to produce only enough males to fertilise her daughters. According to this theory, female thelastomatids should produce only one or few males in mixed-sex batches of eggs. Although thelastomatid males appear to be less common than females in mixed batches of eggs, they are certainly not rare. The reason for this is unknown, but may be linked to the high level of competition between males.

SECTION VI

CONCLUSION

SECTION VI

CONCLUSION

A) MAJOR ACHIEVEMENTS OF THIS STUDY

i) Population self-regulation is shown.

It is generally considered that parasite population regulation results largely from the activities of the host. Host immunity (including concomitant and sterile immunity) is usually invoked to explain parasite distribution patterns. My studies have shown that parasites can regulate their own populations. From this study and from evidence in the literature, I suggest that self-regulation may be important and widespread but not recognised because of masking by immunity. Therefore, the possibility of self-regulation must be considered when mechanisms controlling the population of any parasite are investigated.

ii) Increased fitness is shown to result from self-regulation.

Fitness of individuals is increased as a result of the competitive exclusion of rivals because egg production by uncrowded females is greater than by crowded females.

iii) The predominance of overdispersion amongst parasites is questioned.

I question the widely-held view that overdispersion is the norm amongst parasites. This type of distribution is common amongst parasites of vertebrates, but there is danger in generalisation based only on consideration of such parasites. Much more quantitative work is

needed on the parasites of invertebrates before underdispersion is dismissed as rare.

iv) Inbreeding and the generation of conservative offspring are proposed as thelastomatid strategies and the significance of these phenomena are discussed.

Inbreeding probably occurs amongst thelastomatids as a consequence of batch egg production and arrhenotoky. The significance of this is that co-adapted genes are conserved. For parasites in hosts which have low selection rates (such as cockroaches) the generation of conservative offspring is probably an advantage. This is an antithesis of the nearly universal and more traditional thesis that propagule conservatism and inbreeding are non-adaptive.

B) QUESTIONS RAISED BY THIS STUDY

This work has raised many interesting and challenging questions. Some of these may be answered by future research. Others are theoretical. These questions include:

i) Questions concerning thelastomatid population regulation

a) It is proposed that population regulation results because of nematode-produced anthelmintic(s) (operational definition of anthelmintic - a substance(s) produced by one worm which influences the growth, survival etc. of other worms). What is the biochemical nature of these anthelmintics?

b) How do these anthelmintics work?

c) How are these anthelmintics able to affect one sex but not the other?

d) How do surviving nematodes avoid the lethal effects of these anthelmintics?

e) When a few females in an infrapopulation mature but others of the same age in the same infrapopulation do not, are these juveniles in a state of arrested development similar to that observed in nematodes of ungulates and other mammals?

ii) Questions concerning self-regulation in other host-parasite systems.

a) Does self-regulation play a part in generating dispersion patterns in gut nematodes of hosts other than arthropods?

b) If so, how large a part does self-regulation play, as opposed to say, immmunologically mediated regulation?

c) Does self-regulation occur amongst parasites other than gut parasites?

iii) Questions concerning utility of suspected parasite-produced anthelmintics

a) Could the anthelmintics produced by thelastomatids be manufactured and used to control gut nematodes of medical and veterinary importance?

b) If other parasites self-regulate by producing anthelmintics, could these be used in the same way?

iv) Questions concerning egg production

a) How does crowding operate to reduce fecundity?

b) What controls cyclical egg production?

c) When more than one adult female is present in an infrapopulation, are eggs produced by one, some, or all of them?

v) Questions concerning thelastomatid genetics and reproductive strategies

a) What are the male and female karyotypes of thelastomatids studied?

b) Do all sperm carry chromosomes?

c) Why do some females with access to a male produce both male and female eggs or all male eggs only?

vi) Questions concerning evolution

a) Thelastomatids are arrhenotokous parthenogenes. Arrhenotoky would appear to be less adaptive than thelytoky. Why, then, are thelastomatids arrhenotokous?

b) How common is propagule philopatry and inbreeding amongst parasites other than thelastomatids, and amongst animals and plants in general?

c) What effect does philopatry and inbreeding have on the generation of diversity?

d) If philopatry and inbreeding reduce diversity, how can these phenomena be reconciled with evolutionary theory?

Answers to the questions raised by this thesis will provide new and useful insights into not only thelastomatid biology, but biology in general.

SECTION VII

APPENDICES

Appendix 1. Mean dimensions (μm) of females of species in the genus Protrellus. Some dimensions not available (-), some inferred or arrived at from figures/text. TL, total length; WM, maximum width; LT, tail length; LO, length of oesophagus; LN, anterior to nerve ring; LE, anterior to excretory pore; LV, anterior to vulva; EL, egg length; EW, egg width; OO, shape of oral opening (T, triangular; C, circular); I, isthmus (D, distinct; I, indistinct); EP, excretory pore (ND, not described or figured; S, simple (no lip or flap); L, with lip or flap).

Species	Reference	TL	WM	LT	LO	LN	LE	LV	EL	EW	Egg shape	OO	IS	EP
P. gurri	Dale, 1966	4600	150	450	380	-	250	-	88	42	crested	T	D	ND
P. aureus	Cobb, 1920 Chitwood, 1932 Basir, 1956	6000	100	188	438	-	-	318	104	50	-	T	-	ND
P. galebi	Schwenk, 1926 Chitwood, 1932	6650	235	98	500	184	200	220	75	38	ovoid, laterally grooved	T	D	S
P. kunckeli	Chitwood, 1932 Kloss, 1966	5500	300	233	633	180	-	566	150	85	crested, yellowish brown	-	I	ND
P. australasiae	Chitwood, 1932	2750	220	270	400	-	-	210	76	46	crested, yellowish green	-	I	ND
P. manni	"	2620	100	140	390	-	180	233	95	45	crested, bossed, yellowish brown	-	I	ND
P. aurifluus	"	4300	140	150	330	80	200	211	85	38	crested, yellow	T	I	S
P. phyllodromi	Basir, 1942	2300	160	150	300	130	150	160	75	35	ovoid, laterally grooved	C	I	ND
P. eurycotesi	Kloss, 1961	9500	290	215	500	233	-	300	76	43	crested	C	I	S
P. ischnopteroe	Kloss, 1966	4120	171	54	408	-	-	128	78	36	slight crest	-	I	ND
P. ituana	"	5100	182	155	380	110	-	165	75	36	ovoid	-	I	ND
P. rasolofi	Van Waerebeke, 1969	6950	170	480	462	180	240	290	69	41	ovoid	T	I	L
P. behorefi	"	4545	310	158	411	148	180	205	74	37	crecentric ovoid	C	D	L
P. dalei	Zervos (this thesis)	4166	213	106	414	169	244	273	137	51	ovoid	C	D	L
P. dixoni	"	3767	206	353	408	172	249	288	98	45	ovoid, daffodil yellow	-	D	L

Appendix 2. Mean dimensions (μm) of males in the genus Protrellus. Some dimensions not available, some inferred or arrived at from the figures/text. TL, total length; WM, maximum width; WA, width at anus; LT, length of tail; LO, length of oesophagus; LN, length anterior to nerve ring; LE, length anterior to excretory pore; SL, spicule length; SS, spicule shape (W, well developed capitulum; P, poorly developed capitulum); NP, number of pairs of papillae. Males unknown for P. australasiae, P. manni (Chitwood, 1932); P. phyllodromi (Basir, 1942); P. eurycotesi (Kloss, 1961); P. ischnopterae, P. ituana (Kloss, 1966); P. behorefi (Van Waerebeke, 1969).

Species	Reference	TL	WM	WA	LT	LO	LN	LE	SL	SS	NP
P. gurri	Dale, 1966	550	36	15	11	117	-	120	31	W	4
P. aureus	Cobb, 1920 Chitwood, 1932 Basir, 1956	610	47	-	61	138	61	-	-	P	3
P. galebi	Schwenk, 1926 Chitwood, 1932	270	24	15	34	68	-	-	18	W	3
P. kunckeli	Chitwood, 1932	900	87	-	-	207	-	-	50	W	-
P. aurifluus	Chitwood, 1932	290	18	-	32	73	-	-	17	W	2
P. rasolofi	Van Waerebeke, 1969	755	58	16	39	102	66	160	21	W	3
P. dalei	Zervos (this thesis)	1007	49	22	71	155	85	188	26	P	3
P. dixoni	"	711	39	15	27	127	-	130	22	W	4

Appendix 3. Mean dimensions (μm) of males and females in the genus Blatticola. Some dimensions not available, some inferred or arrived at from figures/text. S, sex (F, female; M, male); TL, total length; WM, maximum width; LT, length of tail; LO, length of oesophagus; LN, anterior to nerve ring; LE, anterior to excretory pore; LV, tail to vulva; EL, egg length; EW, egg width; OO, shape of oral opening (ST, subtriangular; C, circular); IS, isthmus (D, distinct; I, indistinct); SL, spicule length; SS, spicule shape (W, well developed capitulum; P, poorly developed capitulum); NP, number of pairs of papillae; T, testis (O, outstretched; R, reflexed).

Species	Reference	S	TL	WM	LT	LO	LN	LE	LV	EL	EW	OO	IS	SL	SS	NP	T
B. tuapakae	Dale, 1966	F	3760	280	190	390	-	800	500	236	85	C	-	-	-	-	-
		M	960	65	56	150	100	270	-	-	-	ST	-	20	P	3	R
B. blattae	Chitwood, 1930	F	2500	136	200	219	165	750	400	124	40	ST	I	-	-	-	-
	Leibersperger, 1960	M	890	64	70	150	92	250	-	-	-	C	I	20	W	4	0
B. supellaimae	Rao & Rao, 1965	F	3235	301	175	415	195	-	337	162	72	ST	D	-	-	-	-
		M	990	70	50	166	42	-	-	-	-	ST	I	25	P	4	R
B. opisthoplatia	Ahmed & Jabin, 1966	F	2800	400	123	616	318	-	600	254	74	ST	D	-	-	-	-
		M	885	110	35	206	132	-	-	-	-	-	D	42	W	4	O
B. monandros	Zervos, this thesis	F	1949	175	66	333	191	550	299	124	51	C	D	-	-	-	-
		M	668	58	38	178	119	-	-	-	-	-	I	13	P	3	R
B. barryi	Zervos, this thesis	F	2995	316	78	385	231	77	614	175	66	-	D	-	-	-	-
		M	1050	78	50	196	108	-	-	-	-	-	I	20	P	3	R

Appendix 4.

Infrapopulations resulting from feeding 30-50 *P. dixoni* eggs of "unknown" origin (i.e. unknown if donor female nematode came from an infrapopulation with/without a male) to 42 naive adult *D. variegata*. Cockroaches dissected 60 days after start of experiment. Cockroach: No., number of individual cockroach; sex, sex of cockroach. Infrapopulation type: AM, number of adult males; AF, number of adult females; LF, number of juvenile females, in each cockroach. Control cockroaches (n = 12) all uninfected.

Cockroach		Infrapopulation type			Cockroach		Infrapopulation type		
No.	Sex	AM	AF	LF	No.	Sex	AM	AF	LF
1	M	1	2	-	22	F	1	2	2
2	"	1	1	-	23	"	1	2	-
3	"	1	3	-	24	"	1	5	1
4	"	1	2	6	25	"	1	1	-
5	"	1	3	1	26	"	1	3	1
6	"	1	1	1	27	"	1	3	-
7	"	1	3	10	28	"	1	1	-
8	"	1	2	1	29	"	1	2	2
9	"	1	4	2	30	M	1	-	15
10	"	1	1	-	31	"	1	1	17
11	"	1	8	2	32	"	1	-	12
12	"	1	2	2	33	"	-	-	20
13	"	1	2	3	34	"	1	-	14
14	"	1	3	-	35	"	1	-	19
15	"	-	3	5	36	"	1	1	12
16	"	1	3	-	37	"	1	2	15
17	"	1	4	1	38	"	1	-	16
18	"	1	1	-	39	F	1	1	11
19	F	-	2	-	40	"	1	-	22
20	"	1	2	4	41	"	1	-	19
21	"	1	6	2	42	"	1	-	16

Appendix 5.

Chronology of combined experiments investigating P. dixoni infrapopulations in D. variegata resulting from egg(s) from unmated then mated (presumably) female nematodes.

Chronology of experiments:

Day 1. Naive cockroaches given 1 egg each which resulted in 7 hosts having 1-female nematode-infrapopulations (determined by the appearance of eggs in the faeces and by later dissection).

Day 60-90. Nematode eggs collected from faeces of 7 hosts (these resulted in 1-male-only infrapopulations when 1 or many were fed to naive hosts on day 95, dissected on day 125).

Day 90-130. Nematode eggs collected from faeces of 7 hosts, fed back to these 7 hosts on day 135.

Day 170. 7 hosts dissected; each had 1 male - 1 female infrapopulation; 7 now presumably fertilised females fed entire 1 each to 7 naive cockroaches on day 180.

Day 240. 7 cockroaches dissected, nematode infrapopulations found as follows:

Cockroach number	Number of nematodes per infrapopulation		
	Juvenile females	Adult females	Adult males
1	-	2	1
2	-	6	1
3	-	1	1
4	20	-	1
5	11	-	1

Appendix 6. Egg production by Protrellus dixoni in adult D. variegata over a 30 day period. Hosts taken from infected colonies. H, host sex. Nematodes, number of: AF, adult females; AM, adult male (P, present; A, absent); LF, juvenile females. Day, eggs/day (★plotted in Fig. IV. F 1). Eggs: Total, total produced over 30 day period; E/F, eggs per female per day.

H	Nematodes			DAY																													EGGS	
	AF	AM	LF	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Tot.	E/F
m	2	A	3	1	2	6	2	0	0	1	3	8	8	4	0	2	5	7	4	2	3	1	0	2	6	5	4	3	1	0	1	5	4	90	1.5
f	1	P	17	1	0	0	1	2	2	1	0	0	1	0	0	0	1	0	0	0	1	2	1	0	0	0	1	0	0	0	1	0	0	15	0.5
m	1	A	26	3	1	0	0	1	0	0	1	2	0	0	0	2	2	0	0	1	1	0	0	2	3	2	0	0	0	1	0	0	0	21	0.7
m	1	P	6	1	2	10	4	2	0	0	3	4	11	2	0	0	2	9	3	0	1	1	0	0	2	8	7	3	2	1	1	2	2	83	2.77
f	5	P	0	4	1	0	0	0	1	0	0	5	2	0	0	1	0	0	0	0	1	3	0	0	0	0	0	0	1	0	0	0	0	19	0.13
f	8	P	2	★1	3	0	0	0	0	2	1	1	0	0	0	0	0	0	2	3	1	0	0	0	0	0	0	0	1	1	2	1	0★	19	0.08
m	2	P	0	17	7	4	1	1	2	13	2	1	1	0	0	0	2	2	14	11	2	3	0	0	0	0	16	3	4	0	0	2	9	117	1.92
m	1	P	18	5	2	2	1	0	0	0	0	1	6	1	0	0	0	0	2	2	1	9	3	0	0	0	0	1	4	1	1	0	0	42	1.4
m	1	P	30	2	9	2	0	1	0	1	7	1	1	0	0	0	1	0	10	6	2	0	0	0	0	1	9	0	2	0	0	0	0	55	1.83
f	6	A	10	1	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	9	0.05
m	4	P	25	1	0	0	1	2	0	1	1	0	0	3	3	2	3	1	0	1	1	0	2	2	3	5	3	2	1	2	0	0	1	41	0.34
m	1	P	0	5	1	0	0	2	1	1	2	9	3	0	1	1	0	1	0	1	5	11	2	0	0	1	0	0	0	1	1	5	0	53	3.31
f	1	P	2	15	3	2	0	0	0	1	1	3	12	0	0	0	3	21	4	5	1	0	0	0	2	11	3	1	0	0	1	16	2	107	3.57
m	1	P	6	2	18	3	2	0	1	0	0	1	12	4	0	1	0	0	1	15	1	1	1	0	0	12	2	2	0	1	1	3	14	98	3.27
m	2	A	3	2	1	1	0	14	4	0	0	1	9	2	0	0	1	0	1	1	16	2	1	1	0	2	14	2	2	0	0	2	5	84	1.40
m	7	P	7	1	1	0	0	0	2	2	3	1	1	0	0	2	2	5	1	0	0	1	0	0	1	0	1	0	2	0	0	0	0	26	0.12
m	6	P	2	1	0	0	0	1	2	0	1	0	0	0	0	0	0	1	0	2	1	0	0	0	0	1	1	0	0	0	1	3	1	16	0.09
m	5	A	0	3	2	0	0	0	1	3	2	0	0	0	0	0	0	2	4	1	0	0	0	0	0	1	3	1	0	0	0	0	0	23	0.15
f	1	P	1	12	3	1	0	0	1	4	16	3	0	0	0	0	0	1	5	22	2	2	0	0	1	0	0	2	19	6	1	0	0	101	3.37
f	1	P	0	★6	2	2	0	0	3	18	3	2	0	0	5	21	2	1	1	0	0	3	18	2	1	0	0	0	2	19	2	1	1★	115	3.83

SECTION VIII

ACKNOWLEDGEMENTS

SECTION V111

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SECTION IX

REFERENCES

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